FLORA MALESIANA

SERIES II - PTERIDOPHYTA

Ferns and Fern Allies

Vol. 1, part 4 : Lomariopsis Group

LOMARIOPSIS GROUP (R. E. Holttum, Kew)[1]

Aspidiaceae sensu CHING, Sunyatsenia 5 (1940) 247–253, *p.p.*; *Aspidiaceae sensu* COPEL. Genera Filicum (1947) 100–154, *p.p.* — *Dennstaedtiaceae subfam. Lomariopsidoideae* HOLTTUM, J. Linn. Soc. Bot. 53 (1947) 146–149. — *Lomariopsidaceae* ALSTON, Taxon 5 (1956) 25. — *Elaphoglossaceae* PICHI SERM. Webbia 23 (1968) 209–217.

Rhizome creeping or low-climbing (*Bolbitis*) or climbing (*Lomariopsis, etc.*) or epiphytic (*Elaphoglossum*), dorsiventral, with a broad ventral vascular strand which supplies the roots and one or more dorsal strands (the fronds in two or more longitudinal rows, according to the number of strands); *stipes* jointed to rhizome (*Teratophyllum, Elaphoglossum*) or not, containing several separate vascular strands; scales peltate or pseudopeltate, clathrate or not; no elongate unicellular hairs. Rhizomes of *young plants* always with one dorsal meristele, this condition persisting to the adult plant in *Teratophyllum* and many species of *Elaphoglossum*. Fronds simple (*Elaphoglossum, Bolbitis spp.*), pinnate (all but *Elaphoglossum*) or bipinnate (*Teratophyllum* and *Lomagramma spp.*), the pinnae on fronds of *Lomariopsis, Teratophyllum* and *Lomagramma* jointed to the rachis, terminal unjointed lamina present in *Lomariopsis*; distinctive *bathyphylls*, usually more dissected than acrophylls, present in genera with climbing rhizomes (least distinctive in *Lomariopsis*); veins free (*Teratophyllum, Lomariopsis*, most *Elaphoglossum*, some *Bolbitis*) or uniting near the margin (*Elaphoglossum spp.*) or in several series of areoles with (most species of *Bolbitis*) or without (*Lomagramma*; *Bolbitis p.p.*) free veins in the areoles. *Fertile fronds* with reduced lamina, covered beneath (rarely also above) with sporangia (except *Thysanosoria*, where sori are at ends of veins only), a special vascular supply for the sporangia variously developed or not; spores with perispore (except *Lomagramma*).

Genera. *Bolbitis* SCHOTT, *Lomariopsis* FÉE, *Lomagramma* J.SM., *Teratophyllum* METT., *Thysanosoria* GEPP, *Elaphoglossum* J.SM.; also *Peltapteris* LINK (*Rhipidopteris* FÉE *ex* SCHOTT) and *Microstaphyla* PRESL, small genera of tropical America and St Helena, allied to *Elaphoglossum* and not dealt with in the present work.

Taxonomy. In earlier systems species of all genera (except *Thysanosoria*) were included in *Acrostichum* because fertile leaflets are covered beneath with sporangia, without any distinction of separate sori. When PRESL and FÉE distinguished separate genera among such ferns, they depended mainly on venation, and so for example associated *Lomagramma* with the very different genus *Chrysodium* (now known as *Acrostichum s.str.*) because of similarity of venation, and *Egenolfia* and *Bolbitis* (here united as one genus) were placed wide apart because one had free veins and the other anastomosis. JOHN SMITH, who knew a large number of ferns from the living plants he cultivated at Kew, introduced habit of growth, and especially articulation of fronds to rhizome and pinnae to rachis, as additional characters, and thereby made further progress towards a natural system (Historia Filicum 1875).

In CHRISTENSEN's Index Filicum (1905–06), based largely on the system of DIELS in Engler's Pflanzenfamilien (I, Abt. 4, 1899) the genera here included were ranked as follows: *Bolbitis* (excluding free-veined species, *i.e. Egenolfia*) and *Lomagramma* (excluding *L. polyphylla*) were treated as sections of the genus *Leptochilus* in tribe *Aspidieae*; *Egenolfia* was treated as a section of the genus *Polybotrya* (also in *Aspidieae*) and *Teratophyllum articulatum* with *Lomagramma polyphylla* were placed in section *Arthrobotrya* of the same genus; *Lomariopsis* and *Teratophyllum* (apart from *T. articulatum*) were merged with the genus *Stenochlaena* (not even distinguished as sections) in *Blechninae*, a subtribe of *Asplenieae*; the single species of *Thysanosoria* (a name not then established) was included in the genus *Notholaena* in *Pterideae*; *Elaphoglossum* was placed with *Acrostichum* in the tribe *Acrosticheae*.

In CHRISTENSEN's first Supplement to his Index (1913) he recognized *Lomagramma* as a distinct genus, following COPELAND's observations of Philippine *spp.* In 1931 he recognized that *Bolbitis* (under the name *Campium*) and *Egenolfia* are so closely related that they might well be united, and regarded them as 'acrostichoid derivatives from the *Dryopterideae*' (Contr. U.S. Nat. Herb. 26: 291). In 1932 I distinguished *Teratophyllum* and *Lomariopsis* from *Stenochlaena* (Gard. Bull. S. S. 5: 245–312) and demonstrated that the latter is peculiar in growth-habit, venation, anatomy and spores, so that it should belong to another

(1) The treatment of *Bolbitis* is by E. Hennipman, Leyden.

group of genera. In discussing the possible relationships of *Teratophyllum* and *Lomariopsis* I remarked on the similarity of their rhizome-structure and spores to those of *Bolbitis* and *Egenolfia*, suggesting that the four genera, and also *Lomagramma*, formed a natural group (*l.c.* 307–309). In 1938 this conclusion was accepted by CHRISTENSEN (in Verdoorn, Man. Pterid. 545) who regarded all the genera (with the addition of *Thysanosoria*) as acrostichoid derivatives allied to *Dryopteris*. In the same work (p. 549) CHRISTENSEN placed *Elaphoglossum* in a distinct subfamily (of *Polypodiaceae*) of doubtful relationship. CHING emphasized the isolation of *Elaphoglossum* by establishing a distinct family for it (Sunyatsenia 5, 1940, 265). When preparing my fern-flora of the Malay Peninsula, I was struck by resemblances between *Elaphoglossum* and *Lomariopsis*, and added *Elaphoglossum* to the group, which I called *subfam. Lomariopsidoideae* because *Lomariopsis* seemed to be a central genus (J. Linn. Soc. Bot. 53, 1947, 146–149). I placed this subfamily in a family *Dennstaedtiaceae*, not for nomenclatural reasons but because I wished to emphasize the idea that these ferns, and may be others, were likely to have evolved from something like *Dennstaedtia* and that their relationship to *Polypodium* is much more remote, so that the family name *Polypodiaceae* is quite inappropriate for them. In this broader aspect of classification my ideas have now changed somewhat (Brit. Fern Gaz. 9, pt 6, 1965, 205–212) but I still think that these genera form a natural group and that they should not be included in a family named *Polypodiaceae*. ALSTON (*l.c.*) proposed for them the family name *Lomariopsidaceae*, but included formally in his family only the genera found in West tropical Africa. COPELAND (1947) included all genera in his family *Aspidiaceae*, though regarding *Elaphoglossum* as not closely related to the others.

In 1949 I placed subfamily *Lomariopsidoideae* near *Davallioideae* (Bot. Rev. 24: 275, 290). I still think these two groups may be rather closely related, but would not consider them to have had a common origin from ferns like *Microlepia*. Some comments on other possible relationships are given below. The chromosome number 41, found in *Bolbitis*, *Lomariopsis*, *Teratophyllum*, *Lomagramma* and *Elaphoglossum* might indicate an association with *Davallia* or *Ctenitis* or *Dryopteris* (ROY & MANTON, J. Linn. Soc. Bot. 59, 1966, 343–347; T. G. WALKER, Trans. R. Soc. Edinb. 69, 1966, 178).

PICHI SERMOLLI (*l.c.* 1968) has argued that *Elaphoglossum* is not closely related to the other genera, and excluded it from a family *Lomariopsidaceae*. But he based this opinion mainly on a comparison between *Elaphoglossum* and *Bolbitis*, which admittedly are not closely allied. In my original proposal for its present assignment (J. Linn. Soc. Bot. 53, 1947, 149) I expressly compared *Elaphoglossum* with *Lomariopsis*, which I regarded as the central genus of the group. Young plants of most species of *Lomariopsis* (and adult plants of some African species), which have simple fronds, only differ conspicuously from *Elaphoglossum* in lack of articulation of fronds to rhizome. The range of spore-structure in the two genera is similar and I do not think it affords distinguishing characters. However, gametophytes of *Elaphoglossum* do appear to be sharply distinct from those of *Lomariopsis* (though the latter have not as yet been raised to maturity). The two genera have certainly had a long separate history and both are pantropic. Differences in both sporophyte and gametophyte may be due to adaptations to differences of habitat, to which gametophytes are probably more sensitive than sporophytes.

Ecology. The genera may be divided into three groups, according to growth-habits and ecological adaptations.

(1) *Bolbitis* (in Malesia) has short-creeping rhizome (except sometimes in young plants) usually growing on rocks or stream-banks in shady forest, sometimes climbing short distances up tree-trunks but never high-climbing. Pinnae are never jointed to the rachis, there being no need for adaptation to a dry season, but probably fertile fronds are produced in response to somewhat drier conditions.

(2) *Lomariopsis*, *Thysanosoria*, *Teratophyllum* and *Lomagramma*. Young plants start their lives on rocky or earthy banks of streams in tall evergreen forest, or on the exposed roots of trees, always in very humid conditions (some in fresh-water swamp forest), much as *Bolbitis*, but the rhizomes ultimately climb a considerable height up the trunks of trees (never into fully exposed positions), bearing spreading or drooping fronds. In all cases the pinnae are jointed to the rachis and shed when old; this is an adaptation to the high-climbing conditions in which the fronds are in air drier than near the ground (epiphytic orchids all have jointed leaves). In *Teratophyllum* the stipes are rather imperfectly jointed to the rhizome, leaving round scars when shed; in *Lomariopsis* and *Lomagramma* the stipe-bases are decurrent on the rhizome without a joint. In *Lomariopsis* the early fronds are simple and entire (dissected only in *L. variabilis* (WILLD.) FÉE of Mauritius) and are followed by pinnate fronds of increasing size, without any abrupt transition. In *Teratophyllum* the rhizome of a young plant climbing a tree-trunk near the ground has much-divided fronds, here called bathyphylls, of different form in different species, and there is a fairly abrupt transition to the simply pinnate adult condition. In *Lomagramma* young plants creep for some distance on stream-banks (often on rocks) with erect simply pinnate fronds of a distinctive kind, and show a rather abrupt transition to the adult condition, both as regards size of rhizome and of fronds, when they start to climb a tree. In all these genera the plants are rooted in the ground and draw their principal water-supply from the ground. *Thysanosoria* is exactly like *Lomariopsis* in its growth-form as an adult plant and probably resembles *Lomariopsis* in its young stages, though these have not yet been observed.

(3) *Elaphoglossum* species are all normally epiphytic (in Malesia). They have short-creeping rhizomes, to which the fronds are jointed; the joint is rather an imperfect one, between an outgrowth from the rhizome (phyllopodium) and the base of a frond (some American species have no joint). Fronds are thick and fleshly in many cases, especially those growing in more exposed positions in the crowns of trees; those growing near the ground in shade (*e.g. E. melanostictum*) have thinner fronds. The shedding of whole fronds, and their fleshy nature, are adaptations to the epiphytic condition (*Elaphoglossum* fronds are often much like leaves of orchids which grow with them).

The dorsiventral rhizome. The dorsal half of a creeping rhizome of *Bolbitis* has a vascular struc-

ture similar to that of *Dryopteris* or *Tectaria* but the ventral half of the *Bolbitis* rhizome is quite different, being specialized to root-bearing functions and carrying no fronds. There is no doubt that this structure is an advantage to ferns growing on stream-banks and subject to periodic submersion in swift-flowing flood-water. A similar structure is also well-adapted to the high-climbing condition, and to epiphytes which need to be firmly attached to tree-branches; it is found throughout the family *Polypodiaceae* (*s.str.*), the principal group of epiphytic ferns, though *Polypodiaceae* cannot be considered closely allied to the present group of genera.

As indicated below I suggest that the *Lomariopsis* group of genera are related to the *Tectaria* group; if so, they presumably evolved from ancestors with radially organized suberect stems. P. R. BELL has shown that some tropical American species of *Elaphoglossum* have a radially organized stem, though most are dorsiventral, and has found one species in which the change from dorsiventral to radial occurs in the development of a single plant (Ann. Bot. n.s. 19, 1955, 178–180). If one regards all genera of the present group as originating from ancestors with radially-organized rhizomes, BELL's plant indicates a reversion to the ancestral condition; whether all those tropical American species of *Elaphoglossum* which have radially organized rhizomes in the adult plant represent a similar reversion is an open question. It is also an open question whether the dorsiventral condition can have originated on more than one evolutionary line within the group of genera.

NAYAR makes a suggestion as to the origin of a dorsiventral rhizome from a radially symmetrical one, based on "some species of *Tectaria* in which some of the leaves on the ventral side of the procumbent or creeping rhizome are partially suppressed, and are associated with markedly smaller leaf-gaps in the stelar cylinder of the rhizome" (New Phyt. 65, 1966, 237). If such smaller leaf-gaps were completely suppressed a dorsiventral rhizome would result.

Inter-relationships. Assuming that this group of genera had a common ancestor, it was probably a terrestrial fern with dorsiventral creeping rhizome, bipinnate fronds with free veins and a tendency to contraction of fertile leaflets. Changes from this condition were: fronds in most cases to simply pinnate or simple; anastomosis of veins; a high-climbing rhizome and in conjunction with it the articulation of pinnae; loss of indusia and spreading of sporangia to cover the lower surface of reduced fertile leaflets. Some of these changes certainly occurred on more than one evolutionary line. *Bolbitis* represents the evolutionary line (or lines?) in which plants remained terrestrial and pinnae did not become articulated. It is more diversified than any of the other genera, especially in venation; those species which have free veins are primitive so far as that condition is concerned but not necessarily so in other ways.

Rhizome-scales indicate a division of the genera into two groups, those with clathrate scales and those with concolorous scales in which lateral cell-walls are not thickened. (It is notable that *Polypodiaceae s.str.* can also be thus subdivided). *Bolbitis* (in Malesia) and *Lomagramma* have (sub)clathrate scales; fronds of young plants in the two genera also show considerable resemblances. *Lomariopsis*, *Teratophyllum* and *Elaphoglossum* have non-clathrate scales. The bipinnate fronds of *Teratophyllum sect. Polyseriatae* may represent a primitive frond-form. Characters indicating possible cross-relationships between the groups of genera as defined by scales are: fronds of young plants of *Lomariopsis sorbifolia* and some allies in tropical America have much resemblance to those of young plants of *Lomagramma*; and paraphyses in *Lomagramma guianensis* which is of doubtful generic identity are like hairs on the margins of scales of *Lomariopsis*. *Elaphoglossum* is related only to *Lomariopsis*. I regard the development of a joint at the base of the lamina as a separate evolutionary development in this genus; it does not occur in all species (one may compare the orchid genera *Liparis* and *Oberonia*, in which some species have jointed leaves and some have not, the differences being related to the epiphytic condition).

CHRISTENSEN considered the whole group allied to his subfamily *Dryopteridoideae* (in Verdoorn, Man. Pterid. 1938, 545); within the subfamily he suggested a possible affinity of *Bolbitis* with *Tectaria* and its allies. I believe that *Pteridrys* is an ally of *Ctenitis* and *Tectaria*, wrongly placed in the *Thelypteris* group of genera by CHRISTENSEN (*l.c.* 544). The rachis structure and form of attachment of pinnae to rachis are closely similar in *Bolbitis* and *Pteridrys* (HOLTTUM, Rev. Fl. Mal. 2, 1954, 451, 529, fig. 263, 311). The sinus-teeth of *Pteridrys* resemble those of free-veined species of *Bolbitis* (HOLTTUM, *l.c.* fig. 270, 312); and *B. sinensis* (BAKER) K.IWATS. has a frond-form like that of *Pleocnemia* (*sensu proprio*; see HOLTTUM, Reinwardtia 1, 1951, 171–189) which I believe to be closely related to *Pteridrys*. The rachis structure and frond-form of *Dryopteris* are different, and a close relationship of *Bolbitis* to *Dryopteris* is unlikely. A closer study of the whole of CHRISTENSEN's *Dryopteridoideae* and the inter-relations of its parts is still needed.

As regards fertile fronds, the acrostichoid condition is clearly derivative, and within the *Lomariopsis* group (even within *Teratophyllum*) there are various ways in which the vascular system is adapted to it. KAUR (Bot. J. Linn. Soc. 68, 1974, 153) reported that the fertile segments of all lomariopsidoid ferns are provided with a diplodesmic venation; such a pattern is not present in *Bolbitis* (HENNIPMAN, Leid. Bot. Ser. 2, 1977, 35).

The question presents itself: what kind of discrete sori had the ancestors of the group? The little-known genus *Thysanosoria* perhaps gives an indication of the answer; it is so like *Lomariopsis* that the two could not be distinguished in the absence of fertile fronds. It has narrow fertile pinnae with separate sori at the vein-ends, each of which enters a small lobe on the pinna-margin, much as in some species of *Nephrolepis*. *Thysanosoria* sori however lack indusia and the sporangia are distributed a little distance from the end of the vein; a similar spreading has occurred in exindusiate species of many diverse genera which are normally indusiate (*e.g. Tectaria*, *Stegnogramma*). One might therefore postulate an indusiate sorus at a vein-ending as the original fertile state of the group, but not necessarily a lobed margin with sori in the lobes.

It seems possible that the genus *Arthropteris* is more closely related to the *Lomariopsis* group of genera than is *Nephrolepis*. *Arthropteris* resembles *Teratophyllum* in slender climbing rhizome with dorsiventral

structure and two longitudinal rows of fronds on the dorsal surface, also in having the stipes jointed to the rhizome and pinnae to rachis. The jointing of stipe to rhizome is somewhat more definite than in *Teratophyllum*; there are phyllopodia projecting from the rhizome as in *Elaphoglossum* and *Oleandra*. The sori of *Arthropteris* are either indusiate (indusia reniform) or not, for which reason HOOKER placed one species in *Nephrolepis*, one in *Nephrodium* and one in *Polypodium*. The apex of the frond is in some species a terminal lobed lamina continuous with the rachis, in others a jointed pinna as in *Teratophyllum*. The spores have a perispore. The species of *Arthropteris* which most nearly resembles *Teratophyllum* is *A. tenella* (FORST.) J.SM. of New Zealand and Australia; young plants of this species have been reported as having bipinnate fronds (CARSE, Trans. New Zeal. Inst. 47, 1911, 85).

Arthropteris differs from *Teratophyllum* in bearing abundant short multiseptate hairs, much as in *Ctenitis* and *Tectaria*. Such hairs are also abundant in *Davallodes*, a genus allied to *Davallia*, though the latter has almost glabrous adult fronds in all species (SEN, SEN & HOLTTUM, Kew Bull. 27, 1972, 217). Thus *Arthropteris* shows possible relationships to both *Teratophyllum* and *Davallia*; in frond-form of some species it comes near to *Nephrolepis*, in others to *Ctenitis*. I conclude that *Arthropteris* looks like a separate offshoot from the *Ctenitis* stock, not nearly related to *Teratophyllum*, and that, with *Davallodes*, it may indicate relationships between *Ctenitis* and *Davallia*.

Spores of *Lomariopsis* and *Teratophyllum* were first figured by HOLTTUM in 1932 (Gard. Bull. S. S. 5: 252). NAYAR and KAUR have described and illustrated spores of species from all genera in the group (Pollen et Spores 5, 1963, 87–94; J. Palyn. 1, 1965, 10–26). HENNIPMAN (Acta Bot. Neerl. 19, 1970, 671–680; Leid. Bot. Ser. 2, 1977, 38–46) studied several species of *Bolbitis* including some formerly referred to *Egenolfia* with both the transmission and scanning electron microscope. All Malesian species except those of *Lomagramma* have large folded perispore; but see note on species of *Lomariopsis* in Africa and America under that genus. Representative types of perispores are illustrated in fig. 26.

Gametophytes. NAYAR and KAUR (Bot. Rev. 37, 1971, 345–346) summarize published information on gametophytes of *Bolbitis*, *Egenolfia* and *Elaphoglossum*. Dr. L. R. ATKINSON (in Jermy *et al.*, Bot. J. Linn. Soc., Suppl. 1, 1973, 81) has made observations on gametophytes of four species of *Lomariopsis* (1 Malesian, 3 African) and one of *Lomagramma*, also of *Bolbitis spp.* including the American *B. cladorrhizans* (SPR.) CHING (a synonym of *B. portoricensis* (SPR.) HENNIPMAN). Gametophytes of *Elaphoglossum* differ from the other genera in their ribbon-like form with marginal rhizoids; for further comment, see *Elaphoglossum*. Gametophytes of *Lomariopsis* and *Lomagramma* have not yet been raised to maturity. In all cases spathulate young gametophytes are formed with a meristem along the anterior margin, no single apical cell being evident. Gametophytes of *Bolbitis portoricensis* and of *B.* (*Egenolfia*) *hookeriana* IWATS. (a synonym of *B. appendiculata* (WILLD.) IWATS.) are strap-like, those of the Malesian *B. heteroclita* (PRESL) CHING and *B. repanda* (BL.) SCHOTT are broadly cordate and have curved multicellular hairs at the notch and along the anterior margins of the wings; such hairs are lacking in the other species. The sex organs of the lomariopsidoid ferns are of the so-called advanced type. Data on gametophytes, though not offering strong supporting evidence, do not contradict the idea of an alliance between the genera *Lomariopsis*, *Lomagramma* and *Bolbitis*. Gametophytes of *Teratophyllum* have not yet been studied.

KEY TO THE GENERA

1. Fronds of adult plants simply pinnate or bipinnate.
2. Fronds of adult plants simply pinnate.
3. Veins all free.
4. Pinnae jointed to rachis; rhizome high-climbing with widely spaced fronds.
5. Terminal pinna not jointed to rachis at its base.
6. Fertile pinnae covered beneath with sporangia . . . . . **1. Lomariopsis**
6. Sori separate at ends of veins . . . . . **2. Thysanosoria**
5. Terminal pinna jointed at its base . . . . . **3. Teratophyllum**
4. Pinnae not jointed; rhizome short . . . . . **6. Bolbitis**
3. Veins anastomosing.
7. Pinnae jointed to rachis; high-climbing plants . . . . . **4. Lomagramma**
7. Pinnae not jointed; short-creeping plants . . . . . **6. Bolbitis**
2. Fronds of adult plants bipinnate . . . . . **3. Teratophyllum**
1. Fronds of adult plants simple.
8. Veins all free or united at margin only; fronds jointed to phyllopodia . . . . . **5. Elaphoglossum**
8. Veins freely anastomosing; no joint between frond and rhizome . . . . . **6. Bolbitis**

1. LOMARIOPSIS

FÉE, Hist. Acrost. (1845) 10, 66–71, *p.p.*; J.SM. Hist. Fil. (1875) 139; CHRIST, Farnkr. Erde (1897) 39, *p.p.*; HOLTTUM, Gard. Bull. S. S. 5 (1932) 264–277; Not. Syst. 8 (1939) 48–62; Kew Bull. 1939, *n.* 10 (1940) 613–628; TARD.-BL. & C.CHR. Fl. Gén. I.-C. 7, 2 (1939) 427; BACKER & POSTH. Varenfl. Java (1939) 150; COPEL.

Gen. Fil. (1947) 117; Philip. J. Sc. 78 (1949) 400; Fern Fl. Philip. (1960) 267; HOLTTUM, Rev. Fl. Mal. 2 (1954) 476; Blumea 14 (1966) 218. — *Acrostichum sect. Lomariopsis* HOOK. Spec. Fil. 5 (1864) 241, *p.p.* — *Lomariopsis sect. Eulomariopsis* METT. *ex* KUHN, Ann. Mus. Bot. Lugd.-Bat. 4 (1869) 294. — *Stenochlaena sect. Eustenochlaena* DIELS in E. & P. Nat. Pfl. Fam. 1, 4 (1899) 251, *p.p.* — *Stenochlaena sect. Lomariopsis* UNDERW. Bull. Torr. Bot. Cl. 33 (1906) 37, 44–50; v.A.v.R. Handb. (1908) 718, *p.p.*; Suppl. (1917) 427, *p.p.* — **Fig. 1, 26d–e.**

Rhizome climbing, broad, rooting on ventral surface only and bearing several rows (to 5 or 6) of fronds on upper surface, densely scaly on younger parts; scales thin, brown, to 10 by 3 mm, base peltate (or cordate?), edges ± fringed with hairs, lateral cell-walls not thickened; vascular system dorsiventric, showing in transverse section a broadly U-shaped ventral strand and above this a half-ring of wedge-shaped bundles with narrow leaf-gaps between them (fig. 1c). *Stipe* gradually decurrent at base to a ridge on rhizome, free part containing an open ring of *c.* 10 vascular strands, surface scaly when young; *fronds* simply pinnate, pinnae entire, jointed to rachis, terminal lamina pinna-like but not jointed; veins free, usually uniting with the (non-vascular) cartilaginous margin; surface when young bearing scattered minute fimbriate scales. *Pinnae of fertile fronds* much narrower than sterile, their lower surface completely covered with sporangia and small scales as on sterile pinnae; spores large, with copious folded perispore. *Young plants:* rhizome slender, bearing fronds in 2 rows; in Malesian *spp.* fronds simple and usually entire, successively larger to about 30 cm long, later fronds with smaller apical lamina and an increasing number of pinnae; fertile fronds usually not produced until the rhizome is of adult size and has climbed 2 m or more above ground.

Type species: *Acrostichum sorbifolium* L.

Distribution. Throughout the wetter parts of the tropics (America 15 *spp.*, W. Africa & Uganda 10 *spp.*, Islands of Indian Ocean 9 *spp.*, Asia, Malesia, Queensland, and Pacific 10 *spp.*).

Ecology. Plants of primary evergreen forest; prothalli growing on the ground or on exposed roots of trees, the slender rhizome creeping until it meets a tree-trunk, up which it climbs to 5–10 m, retaining a root-system in the ground. As the rhizome grows upwards successive fronds are borne in stronger light and less humid air. Fertile fronds are produced as a response to drier conditions according to local climatic change. Pinnae are deciduous but not whole fronds as *Teratophyllum*. In Luzon M. G. PRICE has found stunted fertile plants creeping on stones in a stream-bed in a semi-exposed position (see *L. lineata*).

Morphology. The broad ± flattened dorsiventral rhizome, ridged on the dorsal surface with decurrent bases of fronds and bearing roots on the ventral surface is exactly as in *Lomagramma*. *Teratophyllum sect. Polyseriatae* differs only in having the bases of stipes a little constricted, not decurrent, and at length deciduous leaving round scars. Young plants of some species of *Lomariopsis* in other geographic regions differ in having fronds which are fully pinnate from an early stage, the terminal lamina never much larger than the lateral pinnae (*e.g. L. sorbifolia* and allied species in West Indies; see HOLTTUM, 1940). In West Africa is one species which has simple fronds throughout its life (*L. palustris* (HOOK.) METT.). In Mauritius *L. variabilis* (WILLD.) FÉE has the early simple fronds more or less deeply dissected (they are comparable to mature sterile fronds of *Peltapteris*). In all cases there is a gradual transition from the frond-form of young plants to that of adult plants, without sharp distinction between bathyphylls and acrophylls.

Gametophytes have not yet been raised to maturity; for available information see p. 258.

Cytology. The only Malesian species investigated is *L. lineata* in cultivation at Kew, from root-tips ($2n = 164$, tetraploid with base 41; ROY & MANTON, J. Linn. Soc. Bot. 59, 1966, 343). Plants from West Africa, also at Kew, gave various different results, and two species also showed unevenness in size of chromosomes.

Spores. In Malesian species the perispore is ± elaborately folded and in some cases is very large (NAYAR, New Phyt. 65, 1966, 235–236); in some species of tropical Africa and America it is not folded, or is produced into numerous small flattened appendages or spines which need to be examined by modern techniques. See fig. 26d–e.

Taxonomy. The genus was founded by FÉE in 1845; he included in it both *Lomariopsis* and *Teratophyllum* of the present treatment (except *T. articulatum*). JOHN SMITH cited *Acrostichum sorbifolium* L. as type species (Hist. Fil. 140, 1875); the choice of *L. cochinchinensis* FÉE by HOLTTUM in 1932, copied by COPELAND (1947) was therefore illegitimate. Most other authors, if they did not follow HOOKER in retaining

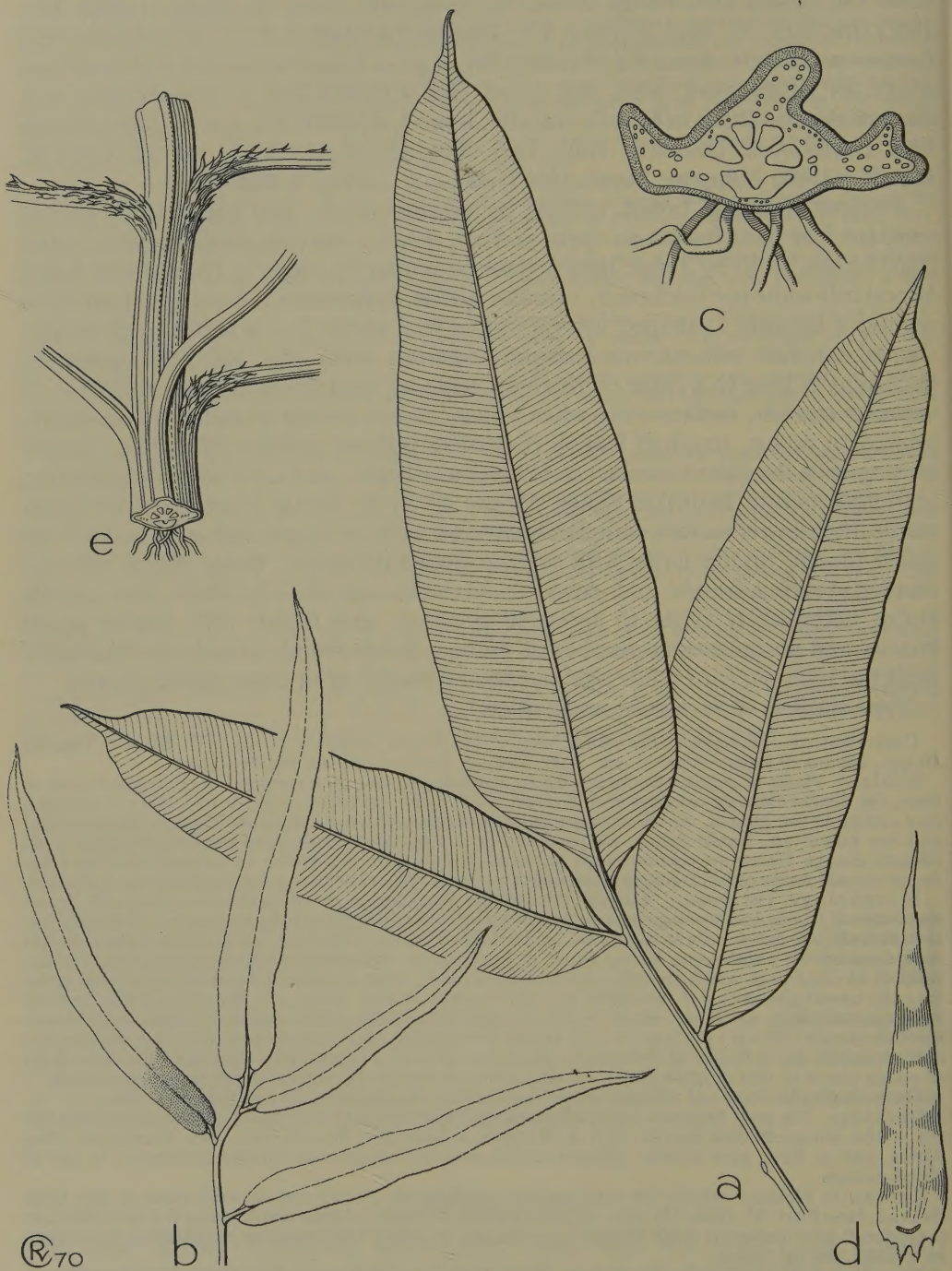

Fig. 1. *Lomariopsis intermedia* (COPEL.) HOLTTUM. *a*. Apex of sterile frond, × $^2/_3$, *b*. apex of fertile frond, × $^2/_3$, *c*. CS of rhizome, × 2, *d*. scale from base of stipe, × 4. — *L. spectabilis* (KUNZE) METT. *e*. Rhizome and decurrent bases of stipes, × $^2/_3$ (*a–d* T. G. WALKER 10064, *e* ENDERT 3785).

FÉE's genus in *Acrostichum*, united it with *Stenochlaena* J.SM. (1841). HOOKER (Spec. Fil. vol. 5) would not recognize most of FÉE's species as distinct and included nearly all of them (including those now separated as *Teratophyllum*) in the single species *A. sorbifolium*. In Farnkräuter der Erde (1897) CHRIST included also in this same species (as *Lomariopsis sorbifolia*) some Asplenioid ferns which have finely dissected fronds in their young stages and simply pinnate in adult condition; in this treatment he was uncritically followed by BOWER (The Ferns 3, 1928, 175–176). In Index Filicum (1906, 625–626) CHRISTENSEN attempted to distinguish twenty "subspecies (vel species?)" within *Stenochlaena sorbifolia*. UNDERWOOD was the first subsequent author to attempt to characterize the species (Bull. Torr. Bot. Cl. 33, 1906, 35–50); he recognized *Lomariopsis* and *Teratophyllum* (excl. *T. articulatum*) of the present work as sections of *Stenochlaena*. HOLTTUM (*l.c.* 1932) pointed out distinctions between *Stenochlaena* and the other two genera in spores, scales, anatomy and venation, and later made observations on *Lomariopsis* in the islands of the Indian Ocean (1939) and tropical America and Africa (1940).

KEY TO THE SPECIES

1. Sterile pinnae very coriaceous, drying brownish; fertile pinnae 10–20 mm wide; spores 90–110 μm long excluding perispore.
2. Stalks of largest pinnae 5–20 mm long; apices of sterile pinnae rather abruptly short-acuminate; veins in sterile pinnae widely spaced and at *c.* 60° to costa . . . . . **1. L. intermedia**
2. Stalks of lowest pinnae always short; apices of sterile pinnae gradually attenuate; veins of sterile pinnae less conspicuous, closer, at their bases almost at right angles to costa. . . . . **2. L. subtrifoliata**
1. Sterile pinnae not very coriaceous, drying dark olive-green; fertile pinnae rarely to 10 mm wide; spores *c.* 45–65 μm long excluding perispore.
3. Upper surface of fertile pinnae not over 2 mm wide; wing of spore narrow, lacking reticulate thickening . . . . . **3. L. kingii**
3. Upper surface of fertile pinnae wider; wing of spore otherwise.
4. Sterile pinnae 3–5 cm wide, on young plants at least abruptly contracted to a short-acuminate apex; spores with ample folded perispore . . . . . **4. L. lineata**
4. Sterile pinnae less than 3 cm wide (usually less than 2 cm), apex always gradually attenuate; spores bearing a perispore of many small wings . . . . . **5. L. spectabilis**

1. Lomariopsis intermedia (COPEL.) HOLTTUM, Gard. Bull. S. S. 5 (1932) 270; COPEL. Philip. J. Sc. 78 (1949) 400. — *Stenochlaena intermedia* COPEL. Philip. J. Sc. 7 (1912) Bot. 67; V.A.V.R. Handb. Suppl. (1917) 429. — Type: C. KING 370, Ambasi, Papua (MICH; dupl. in BM). — **Fig. 1a–d, 26d.**

Rhizome 15 mm or more wide, densely scaly near apex; scales to 10 by 3 mm. *Stipes* to 30 cm long; frond to 70 cm, pinnae to 10 pairs. *Sterile pinnae* 18–35 by $2^1/_2$–5 cm, rather abruptly short-acuminate, conspicuously stalked (stalks of lowest pinnae 5–20 mm long), thick, rigid and brownish when dry, veins to 2 mm apart, simple or once forked, at *c.* 60° to costa. *Fertile pinnae* as long as sterile and similarly stalked, commonly 10–15 mm wide (to 20 mm); spores *c.* 100 μm long excluding perispore which is very wide, elaborately folded, without conspicuous reticulate thickening.

Distr. *Malesia:* eastern half of New Guinea, Louisiade Archipelago.

Ecol. In forest, at 120–1950 m.

Note. This species is near *L. oleandrifolia* (BRACK.) METT. of Fiji. The latter has pinna-stalks $2^1/_2$–$3^1/_2$ cm long, and sterile pinnae very abruptly contracted below the short narrow apex.

2. Lomariopsis subtrifoliata (COPEL.) HOLTTUM, Gard. Bull. S. S. 5 (1932) 274; COPEL. Philip. J. Sc. 78 (1949) 400; Fern Fl. Philip. (1960) 269. — *Stenochlaena subtrifoliata* COPEL. Philip. J. Sc. 1 (1906) Suppl. 152; V.A.V.R. Handb. (1908) 721. (Not *Gymnogramma subtrifoliata* HOOK. 1864 which is *Lomariopsis brackenridgei* CARR.). — Type: COPELAND 1749, San Ramon, Mindanao (MICH).

Similar to *L. intermedia* in rigid sterile pinnae drying brownish and in wide fertile pinnae, differing as follows: pinnae never long-stalked even on large fronds; apices of pinnae gradually attenuate; veins of sterile pinnae closer, starting almost at right angles to costa.

Distr. *Malesia:* Philippines (southern Luzon, Leyte, Samar, Biliran, Mindanao).

Ecol. In forest near streams, at *c.* 800 m.

Note. One specimen from Mt Bulusan has fertile pinnae 8 mm wide, spores 83 μm long.

3. Lomariopsis kingii (COPEL.) HOLTTUM, Gard. Bull. S. S. 5 (1932) 273; COPEL. Philip. J. Sc. 78 (1949) 400. — *Stenochlaena kingii* COPEL. Philip. J. Sc. 6 (1911) Bot. 80; V.A.V.R. Handb. Suppl. (1917) 429. — Type: C. KING 285, Ambasi, Papua (MICH). — **Fig. 26e.**

Rhizome to 12 mm wide; leaf-gaps in vascular system up to 6; young parts and bases of stipes of young fronds densely scaly; scales thin, medium brown, to 10 by 3 mm, edges irregularly hairy when young. *Sterile pinnae* to 20 by $2^1/_2$–3 cm, lower ones on stalks to 5 mm long, base unequally cuneate, widest in basal half, narrowed gradually to acuminate apex (sometimes a rather abrupt narrowing near apex), texture firm. *Fertile pinnae* to 20 cm long, upper surface 2 mm wide (sporangia spreading beyond edges of lamina may produce an apparent width of 3 mm or more); spores 50–65 μm long excluding perispore which is not very wide and has few folds.

Distr. *Malesia:* Philippines (Mindanao to S. Luzon), New Guinea; Queensland.

Ecol. In forest, at 600–2000 m.

Note. This species is very near *L. brackenridgei* CARR. (from which I cannot clearly distinguish *L. setchellii* (MAXON) HOLTTUM) distributed from Fiji to Tahiti, which has even narrower and longer fertile pinnae.

4. Lomariopsis lineata (PRESL) HOLTTUM, Novit. Bot. Inst. Prag. 1968 (1969) 9. — *Olfersia lineata* PRESL, Tent. Pterid. (1836) 235. — *Acrostichum speciosum* PRESL, Rel. Haenk. (1825) 16, *non* WILLD. — Type: HAENKE *s.n.*, Philippines (PRC).

L. cochinchinensis FÉE, Hist. Acrost. (1845) 66, t. 26; HOLTTUM, Gard. Bull. S. S. 5 (1932) 266; TARD.-BL. & C.CHR. Fl. Gén. I.-C. 7, 2 (1939) 428; COPEL. Philip. J. Sc. 78 (1949) 400; HOLTTUM, Rev. Fl. Mal. 2 (1954) 476, f. 279. — *Stenochlaena cochinchinensis* (FÉE) UNDERW. Bull. Torr. Bot. Cl. 33 (1906) 46. — Type: GAUDICHAUD *s.n.* 1827, Tourane, Cochinchina (P; dupl. in B, K).

L. smithii FÉE, Hist. Acrost. (1845) 71, t. 33 f. II (excl. t. s. rhizome), t. 53 f. II; HOLTTUM, Gard. Bull. S. S. 5 (1932) 269; COPEL. Fern Fl. Philip. (1960) 268. — *Stenochlaena smithii* UNDERW. Bull. Torr. Bot. Cl. 33 (1906) 50. — Type: CUMING 143, Luzon (P; dupl. in B, BM, K, L, MICH, US).

Stenochlaena abrupta v.A.v.R. Bull. Jard. Bot. Btzg II, 20 (1915) 24; Handb. Suppl. (1917) 429. — Lectotype: AMDJAH 119, Pladjoe, Borneo (BO; dupl. in L, UC).

L. papyracea COPEL. Philip. J. Sc. 56 (1935) 104, pl. 1 f. 3; Fern Fl. Philip. (1960) 268. — Type: COPELAND *s.n.* 30–8–1932, Mindanao (MICH).

Stenochlaena sorbifolia [*non* (L.) J.SM.] BEDD. Ferns Br. India (1866) t. 192; Handb. (1883) 423 *puoad* f. 254 *tantum*; v.A.v.R. Handb. (1908) 720, *q.p.*

Acrostichum laurifolium [*non* (PRESL) HOOK.] CHRIST, Ann. Jard. Bot. Btzg 15 (1898) 177.

Simple fronds of young plants to 30 by 6 cm, with stipe to 15 cm; lamina abruptly contracted to a narrow apex 2 cm long. *Fronds of mature plant*, including stipe, to 100 cm long, pinnae to 20 pairs. *Sterile pinnae* to 20 by 5 cm, lowest on stalks 5–15 mm long, base narrowly cuneate on basiscopic side, broadly on acroscopic, edges almost parallel for most of length, ± suddenly contracted to a narrow caudate apex 2–3 cm long, edges entire, texture subcoriaceous; upper pinnae often less abruptly contracted near apex. *Fertile pinnae* 8–15 cm long, 3–6(–10) mm wide; spores 43–50 μm long excluding perispore which is wide with reticulate thickening.

DISTR. Tenasserim, S. Thailand, S. Vietnam; throughout *Malesia* except E. New Guinea.

ECOL. In wet lowland forest and to *c.* 1200 m; stunted fertile plants also observed in Luzon creeping on stones in seasonally dry stream-bed.

NOTES. FÉE's figures of *L. smithii* (based on CUMING 143, Luzon) show both fertile and sterile pinnae with very long stalks, but the specimen of this collection at Kew has stalks 3–5 mm long. In Malaya I have found plants growing near together, one with typically broad sterile pinnae, the other with pinnae only half as wide. The type specimen of *L. papyracea* has a normal sterile frond, with a contorted and incomplete fertile one having an apical lamina 16 mm wide; it seems to me improbable that this is a normal frond of a distinct species.

Specimens from Taiwan and Hainan which have been named *L. cochinchinensis* should perhaps be ranked as a distinct species; they are near *L. kingii*, having sterile pinnae $1^1/_2$ cm wide, not abruptly contracted towards apex, and very narrow fertile pinnae.

A specimen consisting entirely of simple fronds, one of them fertile, was collected by M. G. PRICE (463) growing on stones in a seasonally dry streambed in a semi-exposed position, in Camarines Norte Province, southern Luzon. This is the only example of a simple fertile frond of this species seen by me; failure to produce pinnate fronds was doubtless a reaction to the exposed habitat.

5. Lomariopsis spectabilis (KUNZE) METT. Fil. Hort. Bot. Lips. (1856) 22; Ann. Mus. Bot. Lugd.-Bat. 4 (1869) 294, *excl. spec. Zippelii*; HOLTTUM, Gard. Bull. S. S. 9 (1937) 141; TARD.-BL. & C.CHR. Fl. Gén. I.-C. 7, 2 (1939) 428; COPEL. Fern Fl. Philip. (1960) 269 (*p.p.*?). — *Lomaria spectabilis* KUNZE, Bot. Zeit. 6 (1848) 144. — *Acrostichum spectabile* (KUNZE) RACIB. Fl. Btzg 1 (1898) 54, *non* ZOLL. — *Stenochlaena sorbifolia var. spectabilis* v.A.v.R. Handb. (1908) 721. — Type: ZOLLINGER 395, W. Java (L).

Acrostichum smithii RACIB. Bull. Int. Acad. Sci. Lett. Cracovie, Cl. Math. & Nat. B (1902) 59, *non* BAKER. — *Stenochlaena raciborskii* C.CHR. Ind. Fil. (1905) 18, 625 (new name for *A. smithii* RACIB.); v.A.v.R. Handb. Suppl. (1917) 428. — *Stenochlaena smithii* (RACIB.) v.A.v.R. Handb. (1908) 720. — *L. raciborskii* (C.CHR.) HOLTTUM, Gard. Bull. S. S. 5 (1932) 272. — Type: cult. Hort. Bog. origin Moluccas, J. J. SMITH, II.K(V) 23; II.K(XIV) 41 (BO).

Lomaria variabilis (*non* WILLD.) BL. En. Pl. Jav. (1828) 263.

Stenochlaena leptocarpa (*non* FÉE) UNDERW. Bull. Torr. Bot. Cl. 33 (1906) 47 *quoad syn. tantum*; v.A.v.R. Handb. Suppl. (1917) 428, *p.p.*

L. leptocarpa (*non* FÉE) HOLTTUM, Gard. Bull. S. S. 5 (1932) 270. — **Fig. 1e.**

Lamina of *simple fronds* of young plants to 30 by 1.2 cm, narrowed gradually to apex; pinnae of first pinnate fronds sessile. *Fronds of mature plants* 70 cm or more long, pinnae *c.* 15 pairs. *Sterile pinnae* of largest fronds commonly 20 by $1^1/_2$ cm, rarely to $2^1/_2$ or 3 cm wide, lowest with stalks to 10 mm long, apices acuminate (not abruptly narrowed), when dry rigid and brittle, dark olive-green. *Fertile pinnae* to 25 cm long, 4–5 mm wide, stalked as sterile; spores about same size as those of *L. lineata*, perispore consisting of many small wings.

Distr. *Malesia:* Central & South Sumatra, Java, Bali, Borneo, Moluccas; Celebes?; Philippines?.

Ecol. In forest, at 1250–1500 m.

NOTES. *Acrostichum smithii* RACIB. was described from a plant brought from the Moluccas (exact locality unrecorded) by J. J. SMITH. The fronds of the type had few pinnae, sterile ones to 3 cm wide; a later-collected frond, apparently from the same plant, has 6 pairs of pinnae less than 2 cm wide. No other collections are known from the Moluccas.

Specimens from the Philippines formerly referred to this species all appear to have narrower fertile pinnae and I believe they must be regarded as *L. kingii*. Bornean specimens referred here are few and have broad fertile pinnae; their sterile pinnae are thinner and somewhat broader than those of specimens from Java but are narrowly acuminate, not abruptly narrowed near apex as in *L. lineata*. The spores of Kinabalu specimens are somewhat intermediate between those of *L. lineata* and of

typical *L. spectabilis* in form of perispore; but those of ENDERT 3785 from 1200 m in W. Kutai are very like spores of Java specimens.

Excluded

Lomariopsis hügelii PRESL, Epim. Bot. (1851) 263 = *Blechnum filiforme* (A.CUNN.) ETTINGS. Type: HUGEL, New Zealand in Herb. PRESL, seen; duplicate in W. (Not *Stenochlaena hügelii* UNDERW. Bull. Torr. Bot. Cl. 33 (1906) 46 which is *Teratophyllum brightiae* (F.v.M.) HOLTTUM; see Blumea 14 (1966) 218).

2. THYSANOSORIA

GEPP in Gibbs, Dutch N.W. New Guinea (1917) 193, pl. 4; COPEL. Gen. Fil. (1947) 117. — **Fig. 2.**

Like *Lomariopsis* FÉE in habit and in form of sterile fronds, differing in fertile pinnae which have a small rounded marginal lobe at each vein-ending, the sporangia in separate sori, one at the end of each vein and spreading a little backwards along the vein, without indusia.

Distribution. One species, known only from two collections from neighbouring localities in NW. New Guinea, one in 1875, the other in 1913.

Notes. The second collection, as illustrated in GEPP's plate above cited, shows rhizome and frond-characters exactly matching *Lomariopsis*, and I agree with CHRISTENSEN in regarding the two genera as closely related. Possibly the sori of *Thysanosoria* show a stage in the evolution of the acrostichoid condition of *Lomariopsis*. Alternatively, Dr HENNIPMAN suggests that the two specimens named *Thysanosoria* may represent an abnormal condition of a species of *Lomariopsis*; but the collection of identical material after an interval of nearly 40 years is against this. The similarity of the fertile pinnae of *Thysanosoria* to *Nephrolepis* was noted by GEPP; but in vegetative habit and in spores the two genera are very different.

1. Thysanosoria pteridiformis (CESATI) C.CHR. Ind. Fil. Suppl. 3 (1934) 187; Dansk Bot. Ark. 9, 3 (1937) 51; PICHI SERMOLLI, Webbia 32 (1977) 91. — *Gymnogramme pteridiformis* CESATI, Rend. Acad. Napoli 16 (1877) 30. — *Notholaena pteridiformis* (CESATI) BAKER, Malesia 3 (1886) 49; v.A.v.R. Handb. (1908) 484. — Type: BECCARI *s.n.*, Andai (FI, Herb. BECCARI 12704; dupl. in K).

T. dimorphophylla GEPP in Gibbs, Dutch N.W. New Guinea (1917) 193, pl. 4. — Type: L. S. GIBBS 6162 (BM). — **Fig. 2.**

Rhizome as *Lomariopsis*; young parts covered with peltate scales. *Stipe* of sterile frond 7–9 cm long; pinnae to 8 pairs, jointed to rachis, terminal lamina pinna-like but not jointed at its base; pinnae sessile, *c.* 15 cm long, 1.8–2 cm wide, entire, rather thin; veins simple or forked near costa, joining to edge which is pale, slightly thickened and slightly crisped when dry. *Fertile pinnae* 10–15 cm long, 6 mm wide when mature (BECCARI's specimen), edge with a small rounded projection at the end of each vein; sori on distal part of each vein, *c.* 2 mm apart, hemispherical when young. *Spores* with broad winged perispore (width of wing = half diameter of spore) with a few irregular folds.

Distr. *Malesia:* NW. New Guinea.

Ecol. "Common, climbing in karang forest" (GIBBS 6162). Karang is a belt of coral limestone near the coast.

Notes. The two collections differ in the following ways. BECCARI's sterile fronds have only 3 pairs of pinnae, those of GIBBS 6–8 pairs. BECCARI's fertile fronds are old, with pinnae 6 mm wide (Kew specimen; PICHI SERMOLLI reports 7–12 mm), those of GIBBS young and not over 3 mm wide; the latter would have been wider when old, but perhaps not to 6 mm. Sterile plants would look very much like *Lomariopsis kingii*, and it is possible that some

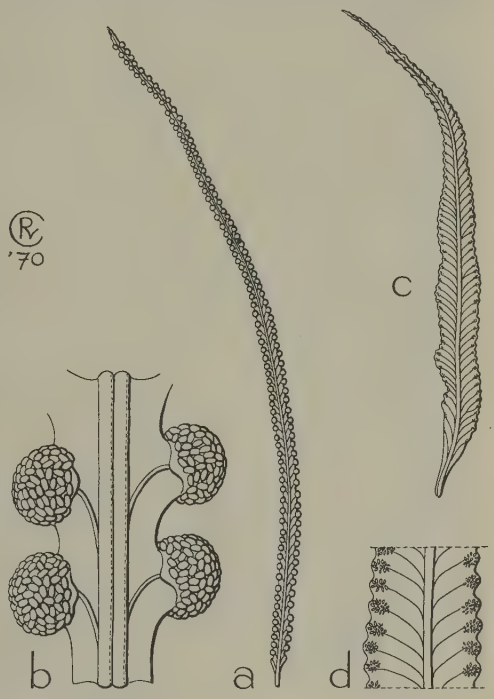

Fig. 2. *Thysanosoria pteridiformis* (CESATI) C. CHR. *a.* Young fertile pinna, × $^2/_3$, *b.* part of *a*, upper surface, showing reflexed sorus-bearing lobes, × 6, *c.* old fertile pinna, × $^2/_3$, *d.* part of *c*, slightly enlarged (*a–b* GIBBS 6162, *c–d* BECCARI *s.n.* 1872).

Fig. 3. *Teratophyllum aculeatum* (BL.) METT. *ex* KUHN. Normal bathyphylls on tree-trunk, Fraser's Hill, Malaya (Photogr. R. E. HOLTTUM).

sterile specimens credited to that species are *Thysanosoria*. The spores of *Thysanosoria* are very much like those of *L. kingii*.

PICHI SERMOLLI (*l.c.*) regarded the collections of BECCARI and GIBBS as representing two distinct species. The differences he cited include number of pinnae, but probably young plants of *Thysanosoria*, like those of *Lomariopsis*, have simple fronds, the number of pinnae in subsequent fronds gradually increasing with decrease in size of the apical lamina; in some cases fertile fronds with few pinnae are produced. As regards differences he described in the fertile pinnae, he failed to note that those on the GIBBS specimen are young and not fully expanded; the apical part of a Kew pinna from BECCARI is not greatly different from the GIBBS specimen in width, and the sori on the BECCARI specimen are not all wholly intramarginal.

3. TERATOPHYLLUM

METT. *ex* KUHN, Ann. Mus. Bot. Lugd.-Bat. 4 (1869) 296; HOLTTUM, Gard. Bull. S. S. 5 (1932) 277–304; *ibid.* 9 (1938) 355. — *Stenochlaena sect. Teratophyllum* UNDERW. Bull. Torr. Bot. Cl. 33 (1906) 37. — **Fig. 3–8.**

Rhizome scandent, dorsiventral, bearing on the ventral surface roots only and on the dorsal surface fronds alternately in 2 rows (*sect. Teratophyllum*) or at maturity in several rows (*sect. Polyseriatae*); bases of stipes swollen and ± articulate to rhizome; rhizome-scales small, peltate, appressed, fugacious, not clathrate. *Fronds* of young plants, or on branches of old plants near ground level (bathyphylls) of a distinctive form characteristic of each species, often bipinnate, with winged rachis and pinnae jointed to it; *fronds of high-climbing rhizomes* (*acrophylls*) larger, simply pinnate (*sect. Teratophyllum*) or sometimes bipinnate (*sect. Polyseriatae*), all pinnae (including the apparently apical one) subequal and jointed to rachis; veins in sterile pinnae or pinnules free, simple or forked; scales small, peltate, with marginal hairs ending in glandular cells; *fertile pinnae* or pinnules much narrower than sterile, their lower surfaces covered with sporangia, the lamina thicker than that of sterile leaflets and containing an additional vascular system close to the surface which bears the sporangia, the strands of this vascular system often anastomosing; paraphyses like the small scales on sterile frond but with a stalk of 5–8 cells; spores with folded perispore.

Distribution. Peninsular Thailand and Lower Burma; throughout Malesia to N. Queensland, eastwards to Tahiti and south to New Caledonia.

KEY TO THE SECTIONS

1. Fronds always in 2 rows on dorsal surface of rhizome; all acrophylls simply pinnate. *Spp.* 1–9 . . . . . **1.** *Sect.* **Teratophyllum**
1. Fronds of fully developed rhizome in more than 2 rows; acrophylls bipinnate or pinnate (in Malesian *sp.* 10 bipinnate) . . . . . **2.** *Sect.* **Polyseriatae**

1. Section Teratophyllum

HOLTTUM, Gard. Bull. S. S. 9 (1938) 355. — *Stenochlaena* J.SM. in Hook. J. Bot. 3 (1841) 401; *ibid.* 4 (1841) 149, *p.p.*; PRESL, Epim. Bot. (1851) 165, *p.p.*; J.SM. Hist. Fil. (1875) 312, *p.p.*; BEDD. Handb. Ferns Br. India (1883) 423, *p.p.* — *Stenochlaena sect. Eustenochlaena* DIELS in E. & P. Nat. Pfl. Fam. 1, 4 (1899) 251, *p.p.* — *Stenochlaena sect. Teratophyllum* UNDERW. Bull. Torr. Bot. Cl. 33 (1906) 37, 40, 41; v.A.v.R. Handb. (1908) 722; Suppl. (1917) 428. — *Lomariopsis* FÉE, Hist. Acrost. (1845) 71, *p.p.*; J.SM. Hist. Fil. (1875) 139, *p.p.*; CHRIST, Farnkr. Erde (1897) 39, *p.p.* — *Acrostichum sect. Lomariopsis* HOOK. Spec. Fil. 5 (1864) 242, *p.p.*; *sect. Stenochlaena l.c.* 249, *p.p.* — *Acrostichum* L. in Racib. Fl. Btzg 1 (1898) 53, *p.p.* — *Teratophyllum* METT. *sensu* HOLTTUM, Gard. Bull. S. S. 5 (1932) 277; *ibid.* 9 (1937)

142; Rev. Fl. Mal. 2 (1954) 470; C.CHR. Ind. Fil. Suppl. 3 (1934) 186; BACKER & POSTH. Varenfl. Java (1939) 151; COPEL. Gen. Fil. (1947) 117; Fern Fl. Philip. (1960) 269.

Type species: *Lomaria aculeata* BL.

Distribution. Mergui and Peninsular Thailand; throughout Malesia, except Lesser Sunda Is.; 9 *spp.*

Ecology. Confined to primary forest. Prothalli grow on exposed tree-roots or bases of buttresses; young sporophytes develop a slender rhizome which usually grows upwards and may branch (in *T. ludens* it produces long trailing branches which pass along the ground from one tree to another) bearing successively larger and more complex bathyphylls, the earlier ones often asymmetric, with lamina more fully developed on lower side, with a more or less abrupt transition to acrophylls at *c.* 2 m above ground level. Fertile fronds produced at 3–5 m or more above ground, seasonally (probably in response to short periods of drier weather, which in many parts of Malesia are of irregular occurrence). A copious root-system develops on the lower parts of the climbing stem, spreading in the soil, and I believe this to provide most of the water needed by the plant. KARSTEN, believing *Teratophyllum* plants to lack such a soil-penetrating root-system, suggested that the chief function of bathyphylls is water-absorption (Ann. Btzg 12, 1895, 143–150). Bathyphylls can absorb some water, but not enough to be of much importance; and they do not always lie in close contact with the bark of the supporting tree, as described by KARSTEN (see fig. 3).

Vegetative morphology. See HOLTTUM, Gard. Bull. S. S. 5 (1932) 277–283. Bathyphylls were formerly considered to be abnormal growths, but they are quite normal, and are distinctive in each species, showing a series of forms from the simple lamina of the first fronds to the pinnate (often bipinnatifid) condition of normal bathyphylls. In the pinnate condition, the lower pinnae are jointed to the rachis but the distal ones are not, becoming merged in an apical lamina. By contrast, all pinnae of acrophylls are jointed at their bases and are caducous; the apparently apical pinna is probably a lateral one which takes a terminal position, the true apex being suppressed. In some cases transition bathyphylls are found, with pinnae much as in normal bathyphylls but all pinnae jointed; I have not seen intermediate stages between these and normal bathyphylls. It seems possible that transition bathyphylls are borne on strong new branches arising near the base of an old plant.

The adult rhizome has always a gutter-shaped root-bearing ventral vascular strand, and a smaller dorsal one (fig. 6j); fronds are borne on the dorsal side, alternately to right and left of the dorsal strand. The arrangement of vascular strands in the stipe is like that on *Dryopteris* and *Tectaria* (fig. 6k). The very narrow fertile pinnae are fleshy, with a special development of vascular strands near the convex sporangia-bearing surface (HOLTTUM, *l.c.*; NAYAR, New Phyt. 65, 1966, 221–239); in the narrower pinnae of *Teratophyllum aculeatum* and other species these strands anastomose rather irregularly, but in the broad fertile pinnae of *T. rotundifoliatum* they do not. Probably such independent vascular supply for the sporangia has evolved independently in various unrelated genera as a necessary adjunct to the acrostichoid state. The fertile pinnae show no indication of an indusium-like thin edge, such as occurs in *Stenochlaena*.

Cytology. The only observation is from roots of a plant of *T. ludens* in cultivation at Kew, showing $2n = 82$.

Taxonomy. The two species native in Java were first described by BLUME (1828) in the genus *Lomaria*; he saw bathyphylls and thought they were fertile fronds. JOHN SMITH, when enumerating CUMING's Philippine ferns (1841) established a new genus *Stenochlaena*, and stated, on the evidence of CUMING's specimens, that *Stenochlaena scandens* (now known as *S. palustris* (BURM. *f.*) BEDD.), the type-species of *Stenochlaena*, sometimes produced abnormal bipinnate fronds. These fronds were bathyphylls of *Teratophyllum aculeatum*, which were associated with normal sterile and fertile fronds of *Stenochlaena palustris* by CUMING under his *n.* 347, as shown by specimens in JOHN SMITH's herbarium (BM), one annotated by him. This idea persisted with SMITH and is repeated in his last book (Hist. Fil. 1875); it was also accepted by HOOKER (Spec. Fil. 5: 250) and by BEDDOME (Handb.) who so named a specimen of *T. aculeatum* bearing bathyphylls collected by WALLICH in Penang in 1822. WALLICH had given the name *Davallia achillaeifolia* to this specimen, and the name was formally published, with a figure, by HOOKER (Spec. Fil. 1: 195), with doubts expressed as to the affinity of the fern and a reference to its resemblance to *Lomaria aculeata* BL. BAKER named similar ferns from Moulmein *Lindsaea parishii* in 1867. Even as late as 1929 COPELAND wrote of "the polymorphism of the fronds of immature plants" of *Stenochlaena palustris* (Univ. Cal. Publ. Bot. 16: 75). Sporeling plants of *S. palustris* are very rare in Malaya, though mature plants are abundant and frequently fertile. I have however raised young plants from spores. Their first fronds were simple, then simply pinnate, showing from the first the leaflet-form and venation of *Stenochlaena*, quite unlike *Teratophyllum*. I can confidently assert that no true *Stenochlaena* produces fronds which could be confused with the bathyphylls of *Teratophyllum*. It should be noted that young plants of *Asplenium epiphyticum* COPEL. also produce bathyphylls. These were confused with those of species of *Teratophyllum* by CHRIST, who concluded that "*Stenochlaena*" was an acrostichoid derivative of Asplenioid origin; COPELAND accepted this derivation as "absolutely clear" in 1929. (See CHRIST, Philip. J. Sc. 2, 1907, Bot. 166; also his earlier composite fig. 96, p. 40, under *Lomariopsis sorbifolia*, which included fronds of *Lomariopsis*, *Teratophyllum* and *Asplenium*, in Farnkr. der Erde, a figure copied without question by BOWER in The Ferns 3, fig. 697).

In his monograph of the acrostichoid ferns (1845) FÉE did not mention *Stenochlaena palustris*. He included the species of *Teratophyllum sect. Teratophyllum* known to him in his new genus *Lomariopsis*; the

species were *L. spinescens* (*Lomaria aculeata* BL.), *L. leptocarpa* (based on CUMING 132 from Luzon) and *L. ludens* (based on a WALLICH specimen from Singapore). Of these, the first was known only from bathyphylls and sterile acrophylls, the second from sterile and fertile acrophylls, the third only from bathyphylls. HOOKER later included all these, and all true *Lomariopsis* specimens known to him, in *Acrostichum sorbifolium* L. (Spec. Fil. 5, 1864, 242), a species now regarded as confined to tropical America.

METTENIUS was the first to recognize *Teratophyllum* as a genus (1869; posthumous work edited by KUHN); he included in it two species, one in each of the sections here recognized (he included *Stenochlaena*, as a section, in *Lomariopsis*). He included all specimens of *sect. Teratophyllum* in the species *T. aculeatum*.

UNDERWOOD clearly distinguished for the first time between *Stenochlaena*, *Lomariopsis* and *Teratophyllum*, ranking all as sections of *Stenochlaena* (Bull. Torr. Bot. Cl. 33, 1906). But he failed to recognize the great differences between *Stenochlaena* proper and the other sections, as he did not examine spores, scales, or vascular anatomy, and failed to notice the "glands" at the bases of pinnae (including basal reduced ones) in *Stenochlaena*; he also failed to notice that *Teratophyllum* differs from *Lomariopsis* in having all pinnae jointed to the rachis, including the apparently terminal one. UNDERWOOD did not recognize the close relationship between *sect. Teratophyllum* and *sect. Polyseriatae*, remarking only that the latter (as *Arthrobotrya* J.SM.) appeared to be a valid distinct genus.

The present account is based on that of HOLTTUM in Gard. Bull. S. S. 5 (1932) 277–304, with some additional material, especially that recently collected by M. G. PRICE in the Philippines.

KEY TO THE SPECIES

Based partly on bathyphylls

1. Pinnae of normal bathyphylls (excluding youngest stages) deeply lobed.
 2. All pinnae of sterile acrophylls almost sessile.
  3. Bathyphyll pinnae to 5 mm wide, pinnules with few segments . . . . . **1. T. aculeatum**
  3. Bathyphyll pinnae to 15 mm wide, pinnules with several segments on each side . . **2. T. gracile**
 2. Lower pinnae of sterile acrophylls with stalks at least 6 mm long, often longer.
  4. Pinnae of bathyphylls deeply dissected to linear lobes.
   5. Ultimate lobes $^1/_3$ mm wide . . . . . **3. T. leptocarpum**
   5. Ultimate lobes much wider. . . . . **6. T. arthropteroides**
  4. Pinnae of bathyphylls less deeply dissected, ultimate lobes almost circular.
   6. Fertile pinnae 3 mm wide . . . . . **4. T. luzonicum**
   6. Fertile pinnae 10 mm wide . . . . . **5. T. rotundifoliatum**
1. Pinnae of bathyphylls (excluding youngest stages) crenate, not deeply lobed.
 7. Most pinnae of sterile acrophylls, and of bathyphylls, very asymmetric at base.
  8. Largest sterile acrophyll pinnae to 9 by 2 cm; basal acrophyll pinnae with almost symmetric base, almost all other pinnae strongly asymmetric; fertile pinnae $4^1/_2$–$5^1/_2$ cm long **6. T. arthropteroides**
  8. Largest sterile acrophyll pinnae to 15 by 2.8 cm; basal acrophyll pinnae strongly asymmetric at base, distal ones much less so; fertile pinnae 20–24 cm long . . . . . **7. T. koordersii**
 7. All pinnae almost symmetric at base, both acrophylls and bathyphylls.
  9. Early stages with lamina on one side of midrib only; small transition bathyphylls with all pinnae on one side of rachis common; fertile pinnae to 20 cm by 3 mm, stalks to 5 mm long . . **8. T. ludens**
  9. Earliest stages with lamina on both sides of midrib; normal and transition bathyphylls all with pinnae on both sides of rachis; fertile pinnae 5–7 cm by 5 mm, stalks 10–15 mm long **9. T. clemensiae**

KEY TO THE SPECIES

Based on acrophyll characters only

1. Pinnae of sterile acrophylls sessile or nearly so.
 2. Sterile pinnae 2–$2^1/_2$ cm wide . . . . . **1. T. aculeatum**
 2. Sterile pinnae 1–$1^1/_2$ cm wide . . . . . **1. T. aculeatum** *var.* **montanum**
  2. T. gracile

1. Pinnae of sterile acrophylls, at least lower ones, stalked.
 3. Bases of some sterile pinnae conspicuously asymmetric.
  4. Stalks of sterile pinnae 3–5 mm long.
   5. Basal pinnae with almost symmetric base, base of others strongly asymmetric; fertile pinnae $4^1/_2$–$5^1/_2$ cm by 5–7 mm . . . . . **6. T. arthropteroides**
   5. Basal pinnae strongly asymmetric at base, bases of upper pinnae less so; fertile pinnae 20–24 cm by $2^1/_2$–3 mm. . . . . **7. T. koordersii**
  4. Stalks of sterile pinnae 5–10 mm long . . . . . **9. T. clemensiae**
 3. Bases of sterile acrophyll pinnae symmetric or nearly so.
  6. Pinnae of sterile acrophylls to 20 by 2 cm . . . . . **3. T. leptocarpum**
  6. Pinnae of sterile acrophylls not over 16 cm long, proportionately wider.

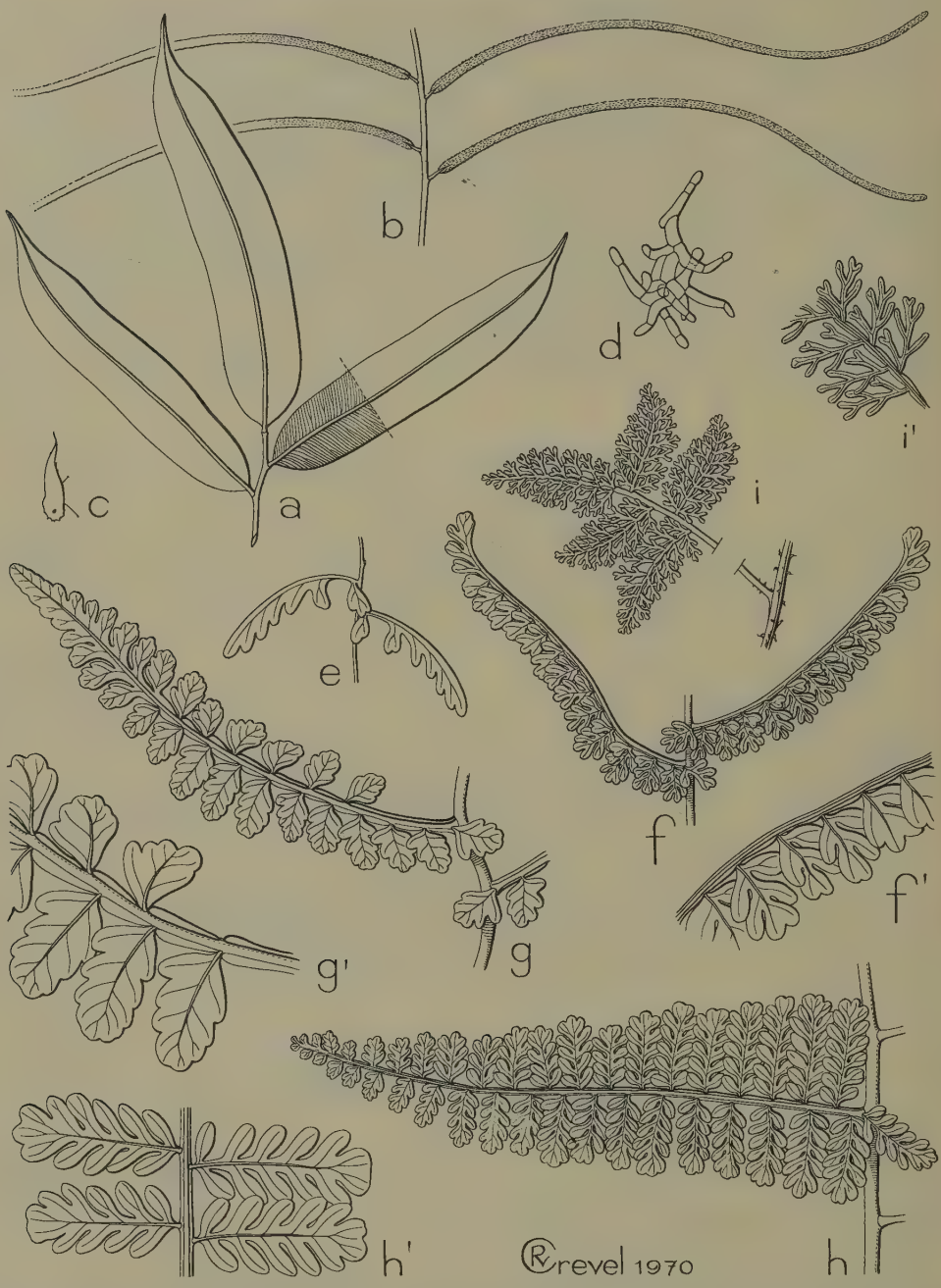

Fig. 4. *Teratophyllum aculeatum* (BL.) METT. *ex* KUHN. *a*. Apex of sterile frond, × ²/₃, *b*. pinnae of fertile frond, × ²/₃, *c*. scale from rhizome, × 4, *d*. scale from bathyphyll, × 80, *e*. earliest stage, *f*. dimidiate normal bathyphyll, both nat. size, *f'*. part of *f*, × 2, *g*. later stage but pinnae less deeply lobed, *h*. mature normal bathyphyll, both nat. size, *h'*. part of *h*, × 2. — *T. gracile* (BL.) HOLTTUM. *i*. Apex of transition bathyphyll, nat. size, *i'*. part of *i*, × 2 (*a–b* KING's Collector 10005, *c–d* DONK *s.n.*, *e* KOSTERMANS 6163, *f* DONK 73, *g* MATTHEW *s.n.*, 28 Jan. 1908, *h* LÖRZING 12257, *i* WINCKEL 1713).

7. Stalks of sterile pinnae to 5 mm long . . . . . **8. T. ludens**
7. Stalks of sterile pinnae to at least 10 mm long.
8. Sides of sterile pinnae parallel except in distal $^1/_3$; fertile pinnae 3 mm wide . . . **4. T. luzonicum**
8. Sides of sterile pinnae not parallel; fertile pinnae *c.* 10 mm wide . . . . **5. T. rotundifoliatum**

1. Teratophyllum aculeatum (BL.) METT. *ex* KUHN, Ann. Mus. Bot. Lugd.-Bat. 4 (1869) 296, *excl. syn. and var. inermis*; HOLTTUM, Gard. Bull. S. S. 5 (1932) 284, f. 32, 38–40, 45, pl. 2, 3; *ibid.* 9 (1937) 144; Rev. Fl. Mal. 2 (1954) 473, f. 276; BACKER & POSTH. Varenfl. Java (1939) 151, f. 29; COPEL. Philip. J. Sc. 78 (1949) 400; Fern Fl. Philip. (1960) 270. — *Lomaria aculeata* BL. Enum. Pl. Jav. (1828) 205. — *Stenochlaena aculeata* (BL.) KUNZE, Bot. Zeit. 6 (1848) 142; KARSTEN, Ann. Jard. Bot. Btzg 12 (1895) 143, t. 14, 15; CHRIST, Philip. J. Sc. 2 (1907) Bot. 166, *p.p.*; v.A.v.R. Handb. (1908) 722, *p.p.*; Suppl. (1917) 430, *excl. var. crassior.* — *Olfersia aculeata* BL. Fl. Jav. Fil. Suppl. (1883?) t. 96. — *Acrostichum aculeatum* (BL.) RACIB. Fl. Btzg 1 (1898) 53, *non* LINN., *nec* DESV. — Type: BLUME *s.n.*, W. Java (L).

Lomaria polymorpha ZOLL. & MOR. *apud* ZOLL. Nat. Geneesk. Arch. N. I. 2 (1845) 204; HASSK. Flora 30 (1847) 319. — Type: ZOLLINGER 2303, Java (BM, BO, L, P).

Davallia achilleifolia WALL. *ex* HOOK. Spec. Fil. 1 (1846) 195, t. 56D; PRESL, Epim. Bot. (1851) 263. — *Acrostichum* (*Stenochlaena*) *scandens* HOOK. Spec. Fil. 5 (1864) 250 *quoad* WALLICH 248 *tantum*. — Type: WALLICH 248, Penang (K).

Lindsaea parishii BAKER, Syn. Fil. (1867) 109; BEDD. Ferns Br. India (1866) t. 209. — *Stenochlaena palustris* BEDD. Handb. Ferns Br. India (1883) 422 *quoad* F.B.I. t. 209 *tantum*. — Type: PARISH 196, Tenasserim (K). — **Fig. 3, 4a–h.**

1. *var.* aculeatum.

Fronds on *young plants* with lamina wholly on one side of midrib, lobed towards the base, later fronds still wholly dimidiate but with lower lobes (to *c.* 20) separate as ± lobed articulated pinnae to 9 by 6 mm (fig. 4f), basal one deflexed across rhizome. *Normal bathyphylls* sessile, glabrous apart from minute scales when young, commonly *c.* 9 by 2 cm (to 12 by 5 cm); pinnae to 5 mm wide, in most cases deeply lobed to a winged costa, basal one deflexed and overlapping rhizome, all jointed to rachis except distal ones which merge with apical lamina. *Transition bathyphylls* variable, some with deeply lobed pinnae (lobes linear), pinnae of others grading to an almost or quite entire condition 12–16 by 5–8 mm with acute or rounded apices. *Adult rhizomes* 4–6 mm diameter, glabrescent except near apex, bearing scattered spines 1–3 mm long; scales near apex abundant, to 2 mm long, narrow, medium brown, base peltate, edges bearing scattered hairs. *Stipes of acrophylls* 3–7 cm long, lamina *c.* 40 cm long with 15 pairs pinnae; *sterile pinnae* sometimes drying reddish (on midrib or throughout), almost sessile (in Luzon lowest pinnae sometimes stalked 3–5 mm), 9–10(–15) cm long, 2–2$^1/_2$(–3) cm wide, base almost symmetric, of lower pinnae sometimes subtruncate, of others broadly cuneate, edges parallel in basal half, apical half tapering, edges minutely sinuous, texture thin, veins distinct, those near pinna-apex ending freely before reaching margin and bearing on both surfaces very small brown fringed scales (abundant on young fronds). *Fertile pinnae* to 15 cm long, hardly 2 mm wide.

Distr. N. to Mergui, throughout *Malesia* except the Lesser Sunda Is.

Ecol. Lowland forest, in moist places; young plants on exposed tree-roots or bases of trunks, climbing to 5 m or more.

2. *var.* montanum HOLTTUM, Gard. Bull. S. S. 5 (1932) 289, pl. 1, 4; Rev. Fl. Mal. 2 (1954) 473. — Type: HOLTTUM 23364, Malaya (K, S).

Differs from *var. aculeatum* as follows: normal bathyphylls often larger (to 16 cm long) with pinnae to 25 by 6 mm, pinnules to 3$^1/_2$ by 2$^1/_2$ mm with forked apex and 2–3 narrow lateral lobes; transition bathyphylls more common and larger; sterile pinnae 8–15 mm wide, sometimes drying reddish.

Distr. *Malesia:* Central & North Sumatra, Malay Peninsula.

Ecol. In forest, in valleys at *c.* 1200–1500 m.

Notes. This is somewhat intermediate between *T. aculeatum* and *T. gracile*. I am not sure that a sharp line can be drawn between *var. aculeatum* and *var. montanum*, but extreme forms of the latter are quite distinct. Most specimens from Taiping Hills have pinnae with narrowly cuneate bases. A specimen from North Sumatra (VAN STEENIS 9724, Mt Kemiri, 1400 m) has bathyphylls intermediate between *var. montanum* and *T. gracile*, and sterile acrophylls like *var. aculeatum*, not narrow as in *T. gracile*.

Aberrant large normal bathyphylls of two distinct types are borne by a few specimens. (a) Fronds 17 cm long, larger pinnae 3$^1/_2$ by 1 cm, segments partly webbed as in many transition bathyphylls, upper pinnae gradually smaller and apical lamina not jointed to rachis (KEHDING 3245, Sumatra, P; ZOLLINGER 2303, Java, L, P). (b) Fronds to 14 cm long, largest pinnae 4 by 1.7 cm, pinnules bipinnatifid (AHERN's collector 2695, Luzon, P, US; WARBURG *s.n.*, Java, P).

2. Teratophyllum gracile (BL.) HOLTTUM, Gard. Bull. S. S. 5 (1932) 291, pl. 5; BACKER & POSTH. Varenfl. Java (1939) 152. — *Lomaria gracilis* BL. En. Pl. Jav. (1828) 205; HOOK. Spec. Fil. 3 (1860) 36. — *Stenochlaena gracilis* KZE, Bot. Zeit. 6 (1848) 142; FÉE, Gen. Fil. (1852) 78; UNDERW. Bull. Torr. Bot. Cl. 33 (1906) 41; v.A.v.R. Handb. Suppl. (1917) 430. — *T. aculeatum* METT. *ex* KUHN, Ann. Mus. Bot. Lugd.-Bat. 4 (1869) 296, *p.p.* — *Olfersia gracilis* BL. Fl. Jav. Fil. Suppl. (1883?) t. 96. — *Acrostichum gracile* RACIB. Fl. Btzg 1 (1898) 53. — *Stenochlaena aculeata sensu* v.A.v.R. Handb. (1908) 722, *p.p.* — Type: BLUME, W. Java (L). — **Fig. 4i.**

Normal bathyphylls to *c.* 12 by 4 cm; pinnae to 12 pairs, to 2$^1/_2$ by 1 cm, pinnate, tapering to apex; largest pinnules 5 mm long, consisting of 2–3 pairs of very narrow lobes (sometimes forked) joined by a very narrow wing. *Transition bathyphylls* to 18 cm long; pinnae 12–15 pairs, to 4 by 1$^1/_2$ cm, with 12 pairs of pinnules; pinnules pinnatisect, largest with 4 pairs of linear lateral lobes 2 mm long, some

forked, ultimate divisions 0.3 mm wide. *Sterile acrophylls* as *T. aculeatum* but pinnae 1–1$^1/_2$ cm wide, dark red when dry. *Fertile pinnae* to 10 cm long, 1–2 mm wide.

Distr. *Malesia:* West Java.

Ecol. In mountain forest, 1000–1500 m.

3. Teratophyllum leptocarpum (FÉE) HOLTTUM, Gard. Bull. S. S. 9 (1937) 143; COPEL. Fern Fl. Philip. (1960) 271. — *Lomariopsis leptocarpa* FÉE, Hist. Acrost. (1845) t. 29. — *Stenochlaena sorbifolia ssp 5* C.CHR. Ind. Fil. (1906) 625, *p.p.* — Type: CUMING 132, Philippines (orig.?; dupl. in B, BM, US).

Stenochlaena williamsii UNDERW. Bull. Torr. Bot. Cl. 33 (1906) 41; CHRIST, Philip. J. Sc. 2 (1907) Bot. 167. — *Stenochlaena gracilis var. williamsii* v.A.v.R. Handb. Suppl. (1917) 431. — *T. williamsii* HOLTTUM, Gard. Bull. S. S. 5 (1932) 292, pl. 6. — Type: WILLIAMS 684, Mt Mariveles, Luzon (MICH, (NY).

Smallest bathyphylls seen 2 cm long, pinnate as normal bathyphylls (not wholly dimidiate as in *T. aculeatum*). *Normal bathyphylls* to 6 cm long, pinnate to base on lower side of rachis, not quite to base on upper side; pinnae to 2 by 1.8 cm, with 4–5 pairs of oblique lateral lobes 3–5 mm long, each lobe pinnatisect with 2–4 linear divisions less than $^1/_2$ mm wide; basal pinnae deflexed, overlapping rhizome. *Transition bathyphylls* to 12 cm long; pinnae to 4 by 1$^1/_2$ cm, lobed as normal bathyphylls but with larger lobes which are more widely spaced; other specimens with lobes of pinnae ± coalescent, pinnae of the extreme form almost sessile with finely crenate edges and broad bases. *Adult rhizome* 4–5 mm ∅, finely thorny. *Sterile acrophylls* with stipes to 20 cm long, lamina 45 cm; pinnae all stalked (stalks of lower ones 6–9 mm), 10–20 cm long, 1–2 cm wide, base slightly unequal, of lower pinnae narrowly cuneate, of upper ones wider, apex long-acuminate, texture rather thin, all parts turning reddish on drying. *Fertile pinnae* to 25 cm long, *c.* 2 mm wide.

Distr. *Malesia:* Philippines (Luzon, Sibuyan, Samar, Panay, Basilan).

Ecol. In forest, especially near rivers, 100–600 m.

Notes. CHRIST (*l.c.* 1907) refers to specimens having "secondary leaves" with a tendency "to present auricles at the anterior base of the pinnules"; these are young plants of an *Asplenium*, probably *A. epiphyticum* COPEL.

The specimen of CUMING 132 at Paris is *Lomariopsis lineata* and is certainly not the one figured by FÉE.

4. Teratophyllum luzonicum HOLTTUM, Gard. Bull. S. S. 5 (1932) 297, pl. 9; *ibid.* 9 (1937) 142; COPEL. Fern Fl. Philip. (1960) 270. — Type: F. FENIX BS 28272, Apayao Prov., Luzon (BO; dupl. in US).

Bathyphylls very like those of *T. rotundifoliatum* (fronds 1$^1/_2$ cm long not dimidiate); transition bathyphylls bipinnate, larger pinnules with one rounded or slightly bifid lobe on acroscopic side. *Adult rhizome c.* 4 mm ∅, somewhat spiny. *Sterile acrophylls* to 60 cm long including stipe, with 8 or more pairs of pinnae; pinnae to 15 by 3 cm, on stalks to 12 mm long, base broadly and slightly unequally cuneate, sides nearly parallel except in distal third, apex acuminate, texture firm, drying green, veins near midrib 1$^1/_2$–2 mm apart. *Fertile acrophylls* with pinnae to 10 cm long and 3 mm wide, on stalks to 5 mm long.

Distr. *Malesia:* Philippines (Luzon, Palawan, Mindanao).

Ecol. At 600–700 m (JACOBS 7944, Sierra Madre Mts; sterile and fertile acrophylls).

Note. No bathyphylls were collected in association with the original specimens. I subsequently described bathyphylls from Palawan, some of which were associated with sterile acrophylls. There are also transition bathyphylls which in 1937 I thought represented *T. clemensiae*, but now I think it more likely that they also belong to *T. luzonicum*. A final proof can only come from a collection of all stages from the same place. The fertile fronds of *T. luzonicum* and *T. clemensiae* are very different. There are also bathyphylls, without acrophylls, in a collection by LOHER from Mt Mariveles; these agree well with Palawan specimens.

5. Teratophyllum rotundifoliatum (R.BONAPARTE) HOLTTUM, Gard. Bull. S. S. 5 (1932) 294, pl. 7, 8, f. 36, 37, 44; Rev. Fl. Mal. 2 (1954) 474, f. 277. — *Stenochlaena rotundifoliata* R.BONAP. Notes Ptérid. 14 (1923) 58. — Type: HOLTTUM 9384, G. Lambak, Johore (P; dupl. in SING).

Stenochlaena aculeata var. crassior v.A.v.R.Bull. Jard. Bot. Btzg II, 23 (1916) 20; Handb. Suppl. (1917) 430. — Type: AJOEB 387, Bencoolen, S. Sumatra (BO). — **Fig. 6f–k.**

Earliest stage as *T. clemensiae* (not dimidiate as in *T. aculeatum*), the entire fronds soon succeeded by bipinnatifid *normal bathyphylls* up to 8 by 3$^1/_2$ cm, with closely-placed pinnae to 15 by 4 mm with almost circular pinnules, texture firm, usually drying light green. *Transition bathyphylls* to 15 by 6 cm, with up to 20 pairs of pinnae more widely separated than in normal bathyphylls, pinnae to 30 by 4 mm, coriaceous, deeply lobed, lobes *c.* 2 mm wide, apices rounded, retuse or bilobed. *Adult rhizome* to 8 mm ∅, strongly aculeate, when young densely covered (also young fronds) with small red-brown scales, largest scales seen 7 by 1 mm. *Sterile acrophylls* to 60 cm long including stipe, with 12 pairs of pinnae; all pinnae stalked (stalks of lowest 10–15 mm), commonly to 15 by 3 cm (largest seen 16 by 6 cm), widest below middle, gradually tapering to apex, base rather broadly and almost equally cuneate, coriaceous, drying light green. *Fertile pinnae* to 10 by 1 cm, on stalks to 18 mm long; tips of veins not connected by a submarginal vein.

Distr. *Malesia:* Central & South Sumatra, Malay Peninsula, Borneo.

Ecol. In forest on hillsides (not in swamp-forest), at 150–1000 m.

Note. The only known fertile specimens were collected by WRAY (679, K, SING) in Perak; they are young, with immature sporangia. This species differs from *T. clemensiae* in the broader fertile pinnae without marginal vein, coriaceous sterile pinnae, and in invariably bipinnatifid bathyphylls after the earliest stages. Spores have not been seen.

6. Teratophyllum arthropteroides (CHRIST) HOLTTUM, Gard. Bull. S. S. 5 (1932) 303, pl. 12; COPEL. Fern Fl. Philip. (1960) 271. — *Stenochlaena*

arthropteroides CHRIST, Bull. Herb. Boiss. II, 6 (1906) 998; Philip. J. Sc. 2 (1907) Bot. 167; v.A.v.R. Handb. (1908) 719. — Type: LOHER *s.n.* April 1906, Rio Ampalit, Mt Makiling, Laguna Prov., Luzon (P). — **Fig. 5a–c.**

On all *bathyphylls* seen (smallest 4 cm long) all pinnae articulate; largest seen 12 cm long with 6 pairs pinnae and stipe nearly 2 cm long; pinnae 10 by 5 to 30 by 12 mm, base narrowly cuneate on basiscopic side, broadly on acroscopic, edges crenate, apex blunt; on one collection most pinnae deeply lobed. *Adult rhizome* smooth. *Sterile acrophylls* to 40 cm long; rachis usually reddish when dry; pinnae stalked (stalk of lowest 3–4 mm), 5–9 cm long, $1^1/_2$–2 cm wide, basal pinnae with symmetric base, rest with base very unequal (basiscopic narrowly cuneate, acroscopic subtruncate), tapered gradually from widest part near base to acuminate apex, texture thin, edges in most cases distinctly crenulate (one crena to each vein-end). *Fertile fronds* shorter than sterile, pinnae $4^1/_2$–$5^1/_2$ cm long, 5–7 mm wide.

Distr. *Malesia:* Philippines (Luzon, Mindanao).

Ecol. In forest, at 250–400 m.

Note. I have not seen the youngest stage of this species. Small transition bathyphylls are very like those of *T. koordersii* but thinner, and those seen have a distinct stipe so that basal pinnae do not overlap the rhizome.

7. Teratophyllum koordersii HOLTTUM, Gard. Bull. S. S. 5 (1932) 301, f. 48, 49, pl. 11. — Type: KOORDERS 17065, Minahassa, N. Celebes (BO). — **Fig. 5d.**

Youngest stage: fronds up to 3 cm long dimidiate with 3 free pinnae all on lower side of rachis (rarely 1 leaflet or lobe on upper side); fronds 3 cm long and larger dimidiate with jointed apical pinna, pinnae 4, to 10 by 3–5 mm, base asymmetric, edges crenate to deeply lobed; *later bathyphylls* with pinnae both sides, on a frond $7^1/_2$ cm long apical pinna 20 by 8 mm, lateral pinnae 6 pairs, crenate, decreasing downwards, lowest 13 by 6 mm, base narrowly cuneate on basiscopic side, broadly on acroscopic. *Intermediate fronds* 14 cm long, pinnae 8–9 pairs, apical one 3.8 by 1.4 cm, edges almost entire. *Adult rhizome* 4–5 mm ∅, aculeate. *Sterile acrophylls:* stipe $5^1/_2$ cm, lamina 45 cm, pinnae 11–12(–20?) pairs, to 15 by 2.8 cm, lowest stalked 5 mm, basiscopic base narrowly cuneate, acroscopic broadly rounded, upper pinnae with more symmetric bases. *Fertile fronds:* pinnae 20–24 cm long, $2^1/_2$–3 mm wide, stalks to 5 mm long.

Distr. *Malesia:* N. Celebes, Philippines (Luzon).

Ecol. In moist forest, low altitude.

Note. The above description is taken in part from specimens collected in Luzon by M. G. PRICE (*nos* 927, 928, 940, 958, 979, 981). These agree closely with the Celebes type and two other speci-

Fig. 5. *Teratophyllum arthropteroides* (CHRIST) HOLTTUM. *a*. Upper pinnae of sterile acrophyll, *b*. bathyphylls, *c*. fertile pinnae. — *T. koordersii* HOLTTUM. *d*. Bathyphylls. All × $^2/_3$ (*a* ELMER 18353, *b–c* COPELAND PPE 251, *d* KOORDERS 17064).

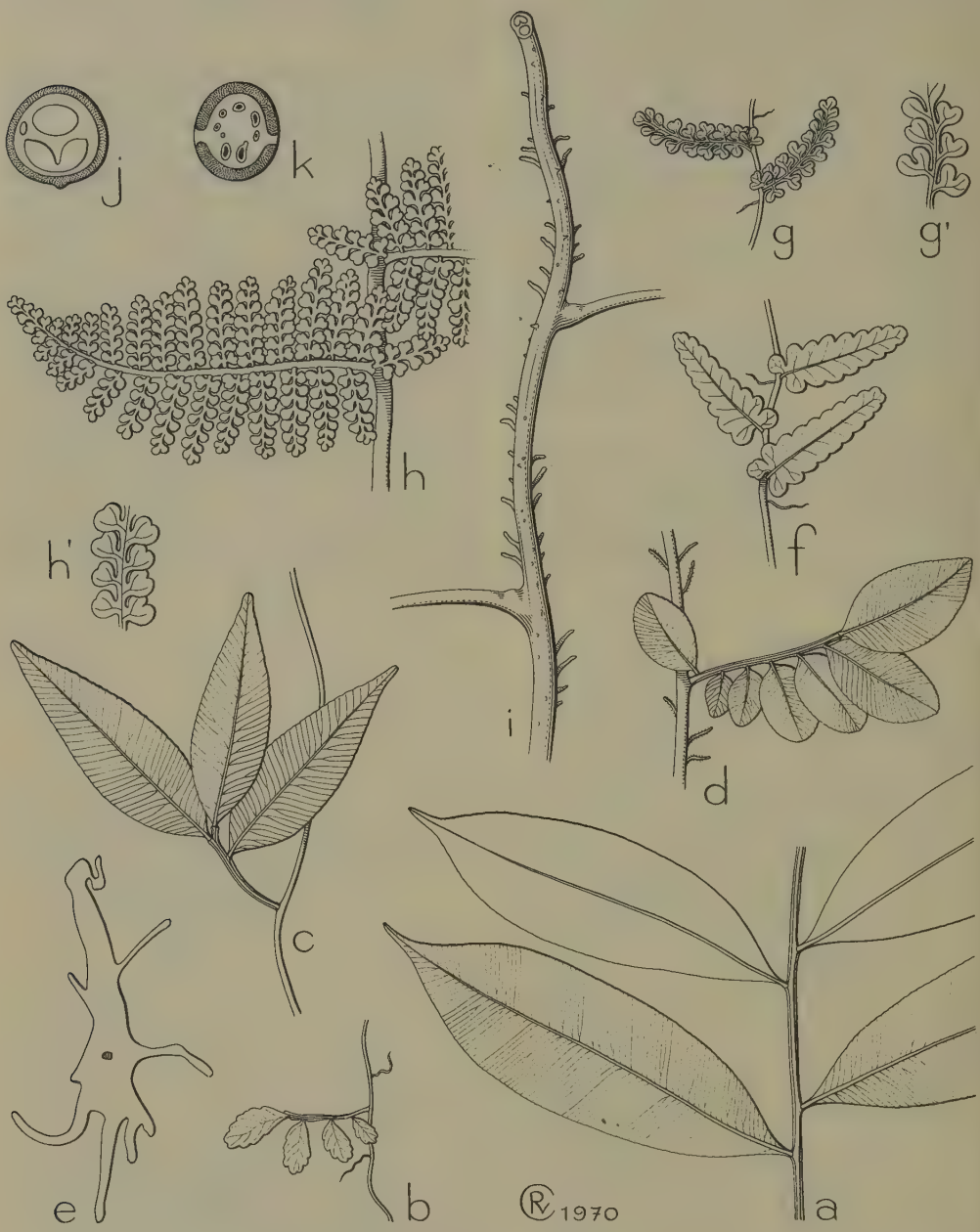

Fig. 6. *Teratophyllum ludens* (FÉE) HOLTTUM. *a*. Pinnae of sterile acrophyll, *b*. bathyphyll, early stage, *c*. bathyphyll from creeping rhizome, *d*. bathyphyll from climbing rhizome, all × $^2/_3$, *e*. scale from base of stipe, × 40. — *T. rotundifoliatum* (R. BONAP.) HOLTTUM. *f*. Earliest stage, *g*. second stage, both nat. size, *g'*. part of *g*, pinnae not jointed to rachis, × 2, *h*. mature bathyphyll, nat. size, *h'*. part of a pinna from *h*, × 2, *i*. rhizome and stipe-bases, × $^2/_3$, *j*. CS of rhizome, *k*. CS of stipe, both × 4 (*a* HOLTTUM *s.n.*, 13 Oct. 1929, *b* POLAK 301, *d* HOLTTUM 24632, *f–g* CORNER 29215, *h–i* WRAY 679, *e*, *j*, *k* from Gard. Bull. S. S. 5, 1932, 278, 279).

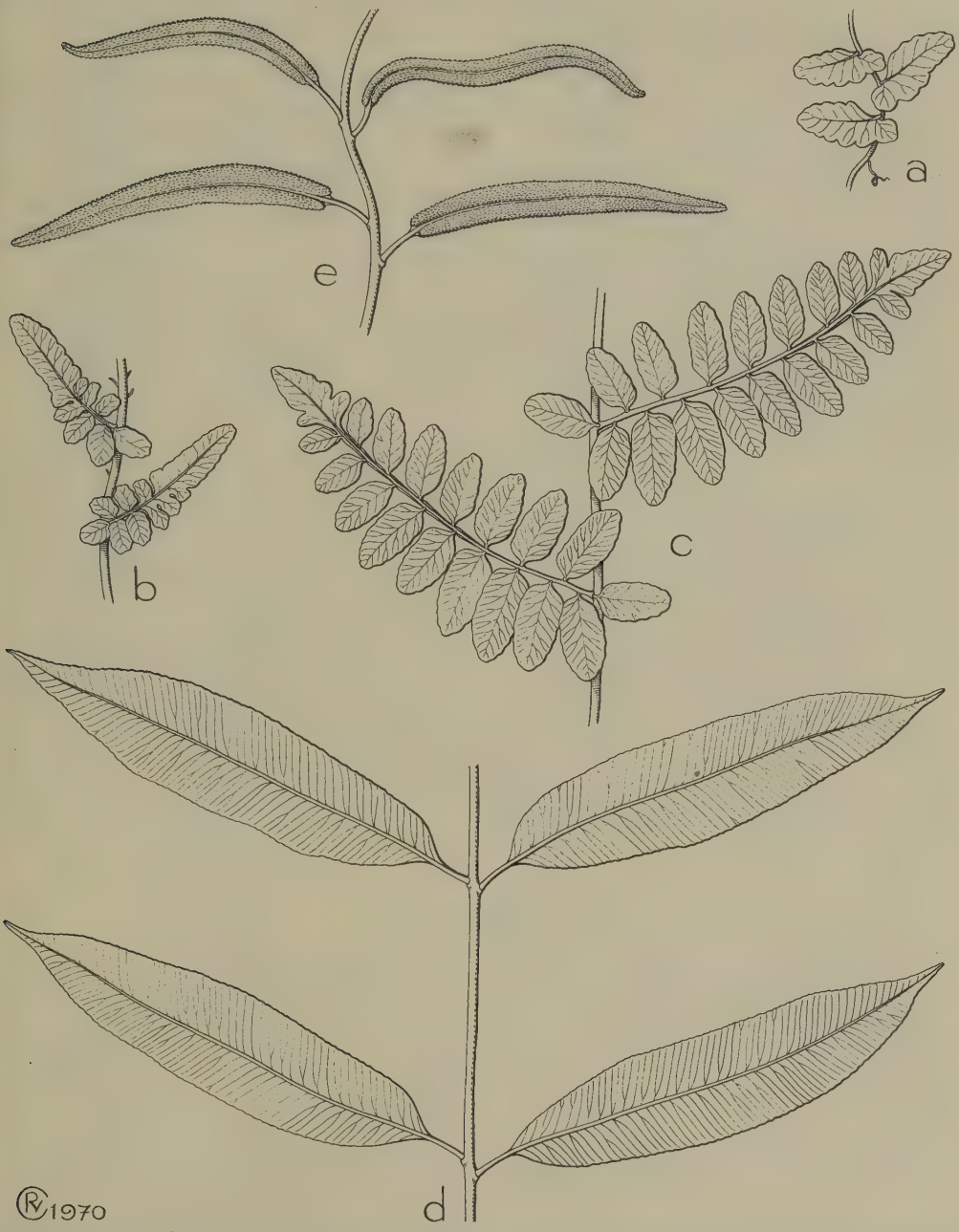

Fig. 7. *Teratophyllum clemensiae* HOLTTUM. *a*. Earliest stage, *b*. second stage, *c*. mature bathyphylls, *d*. pinnae of sterile acrophyll, *e*. pinnae of fertile acrophyll, all × $^{2}/_{3}$ (*a* CLEMENS 30890, *b* CLEMENS 50592, *c* CLEMENS 40560, *d–e* CLEMENS 31346).

Fig. 8. *Teratophyllum articulatum* (J. SM. *ex* FÉE) METT. *ex* KUHN. *a*. Sterile acrophyll and rhizome, × 1/3, *b*. one pinna of sterile acrophyll, *c*. fertile pinnules, *d*. frond of young plant, second stage, basal pinna pinnate, all × 1/2, *e*. rhizome with base of stipe, × 1/3, *f*. CS of rhizome, × 2, *g*. bullate scales from rachis of acrophyll, × 16 (*a* BAMLER in Rosenst. Fil. Novog. exsicc. 122, *b*, *e–g* BRASS 12202, *c* CLEMENS 1073, *d* EDAÑO 15165).

mens from the original locality in details of bathyphylls and sterile acrophylls. The fertile specimen (PRICE 927) was found on a high-climbing plant on the edge of forest, not associated with bathyphylls; no fertile fronds are known from Celebes.

8. Teratophyllum ludens (FÉE) HOLTTUM, Gard. Bull. S. S. 5 (1932) 298, pl. 10, f. 35, 46, 47; Rev. Fl. Mal. 2 (1954) 474, f. 278; TAGAWA & IWATSUKI, Act. Phytotax. Geobot. 24 (1970) 62. — *Lomaria ludens* FÉE, Hist. Acrost. (1845) 70, t. 30. — Type: GAUDICHAUD *s.n.* 1836–37, Singapore (P).

Without name, BEDD. Ferns Br. India (1866) t. 210. — *Stenochlaena sorbifolia* [*non* (L.) J.SM.] BEDD. Handb. (1883) 423, *quoad* F.B.I. t. 210 *tantum*. — Type: PARISH *s.n.* 1863, Mergui (K).

T. aculeatum var. inermis METT. *ex* KUHN, Ann. Mus. Bot. Lugd.-Bat. 4 (1869) 297. — **Fig. 6a–e.**

Earliest fronds almost as *T. aculeatum*, with triangular lamina, deeply lobed or with free pinnae at base, on one side of midrib only. *Transition bathyphylls* on climbing stems $2^1/_2$–$7^1/_2$ cm long; pinnae 5–9, apical one largest, all on side of rachis towards ground and standing away from supporting tree to which rachis is closely appressed; pinnae 5–30 mm long, broadly elliptic or ovate, apices rounded, edges crenulate distally; later fronds of this type may have 1–2 pinnae on upper side, towards apex; fronds on stems which creep on the ground very variable, bearing (on both sides of rachis) few subequal larger pinnae which are in some cases widest near base, tapering gradually, no basal pinnae overlapping rhizome. *Rhizome* of adult plant *c.* 3 mm ∅, not aculeate. *Sterile acrophylls* to 50 cm long including stipe; pinnae to 10 pairs, lower ones with stalks to 5 mm long, upper sessile, 7–12 cm long, 2–$4^1/_2$ cm wide, firm, drying light olive green, almost elliptic or with edges parallel in middle part, narrowed about equally to broadly cuneate base and abruptly short-acuminate apex; veins near midrib 1–$1^1/_2$ mm apart; edges slightly sinuate, narrowly cartilaginous. *Fertile fronds* as long as sterile; pinnae to 20 cm long, 3 mm wide, on stalks to 5 mm long.

Distr. Peninsular Thailand and Tenasserim (N. to Mergui); in *Malesia:* Malay Peninsula, Borneo (Sarawak).

Ecol. In fresh-water swamp forest.

9. Teratophyllum clemensiae HOLTTUM, Gard. Bull. S. S. 7 (1934) 262, f. 1–9 (not *ibid.* 9, 1937, 142, which refers to *T. luzonicum*). — Type: CLEMENS 31614, N. Borneo, Mt Kinabalu, Penibukan (SING). — **Fig. 7.**

Simple fronds on very young plants to 3 by $1^1/_2$ cm, base on lower side broadly cordate and overlapping rhizome, on upper side cuneate, edges sinuate, apex broadly rounded. Smallest *normal bathyphylls* narrowly deltoid, $4^1/_2$ by 2 cm, with 3 or 4 pairs of jointed pinnae below deeply lobed triangular apex, pinnae elliptic, entire, apex rounded, base unequally cuneate; largest fronds to 9 by 4 cm with 9 pairs of free pinnae 2.2 by 1 cm somewhat narrowed to rounded apex. *Transition bathyphylls* of various types, all with entire pinnae shaped nearly as acrophylls; pinnae in some cases all on one side of rachis, usually on both sides, largest fronds to 18 cm long with 10 pairs of pinnae on stalks to 3 mm long, lowest pinna always deflexed, overlapping rhizome. *Rhizome* of adult plant 5 mm ∅ with short spines. *Sterile acrophylls* 40–70 cm long including stipe 5–15 cm; pinnae *c.* 10 pairs, stalks 5–10 mm long, blade 8–15 cm by $1^1/_2$–$2^1/_2$ cm, broadest near unequally cuneate base, tapering gradually to acuminate apex, texture thin but firm, drying rather light green, veins *c.* 2 mm apart near midrib, margin narrowly cartilaginous and regular sinuous (prominences at vein-ends). *Fertile fronds* with 10–12 pairs of pinnae on stalks 10–15 mm long; each pinna 5–7 cm long, 5 mm wide, veins uniting in a submarginal vein.

Distr. *Malesia:* Borneo (Sarawak & Sabah).

Ecol. In forest, at 600–1500 m.

NOTE. In 1937 I suggested that transition bathyphylls from Palawan (MERRILL 862, US) were referable to this species. I now think that they are more likely to belong to *T. luzonicum*, as their pinnae have a more oblong shape and veins closer together than in bathyphylls of this size in *T. clemensiae*.

2. Section Polyseriatae

HOLTTUM, Gard. Bull. S. S. 9 (1938) 356; Blumea 14 (1966) 216–218. — *Polybotrya sensu* FÉE, Hist. Acrost. (1845) 12, 72, *p.p.* — *Acrostichum sect. Polybotrya* HOOK. Spec. Fil. 5 (1864) 247. — *Teratophyllum* METT. *ex* KUHN, Ann. Mus. Bot. Lugd.-Bat. 4 (1869) 297, *p.p.* — *Arthrobotrya* J.SM. Hist. Fil. (1875) 141; UNDERW. Bull. Torr. Bot. Cl. 33 (1906) 40; COPEL. Gen. Fil. (1947) 118; Fern Fl. Philip. (1960) 272. — *Polybotrya sect. Teratophyllum* CHRIST, Farnkr. Erde (1897) 42; DIELS in E. & P. Nat. Pfl. Fam. 1, 4 (1899) 198. — *Polybotrya sect. Arthrobotrya* v.A.v.R. Handb. (1908) 725. — *Lomagramma sensu* COPEL. Philip. J. Sc. 3 (1908) Bot. 32, *p.p.*; C.CHR. Ind. Fil. Suppl. 1 (1913); v.A.v.R. Handb. Suppl. (1917) 437.

Type species: *Polybotrya articulata* J.SM. *ex* FÉE.

Distribution. Malesia: Celebes, Moluccas, Philippines, New Guinea; eastwards to Tahiti, southeastwards to Queensland and New Caledonia; 3 *spp.*

Vegetative morphology. See HOLTTUM, *l.c.* Acrophylls of the Malesian species *T. articulatum* are always bipinnate; in *T. wilkesianum* (BRACK.) HOLTTUM (New Caledonia to Tahiti) some acrophylls (both

sterile and fertile) are simply pinnate, and not infrequently one frond is partly pinnate, partly bipinnate; in *T. brightiae* (F.v.M.) HOLTTUM (N. Queensland) all acrophylls are simply pinnate. Detached simply pinnate acrophylls, whether sterile or fertile, are indistinguishable from such fronds of *sect. Teratophyllum*. The youngest stages of bathyphylls are inadequately known; one specimen of a young plant of *T. articulatum* has bipinnate fronds with deflexed basal pinna, not differing in any significant character from *sect. Teratophyllum*. The bathyphylls of *T. brightiae* are always simply pinnate (HOLTTUM, 1938, pl. 28) but the earliest stage is not known. Vascular anatomy of adult rhizomes is very like that in *Lomariopsis*, but the bases of stipes are somewhat swollen and rather imperfectly jointed, not gradually decurrent as in *Lomariopsis*. Fertile leaflets have an additional vascular supply for the sporangia, as in *sect. Teratophyllum*.

Taxonomy. As indicated in the synonymy, *T. articulatum* was first included in the genus *Polybotrya* HUMB. & BONPL. and transferred to the new genus *Teratophyllum* by KUHN in 1869. JOHN SMITH established a new genus *Arthrobotrya* for it in 1875, but CHRIST and DIELS retained it in *Polybotrya sect. Teratophyllum*, in which they did not include the species here placed in *Teratophyllum sect. Teratophyllum*. The second species of the section, *T. wilkesianum*, was described in *Polybotrya* by BRACKENRIDGE in 1854, the third, *T. brightiae*, by F. VON MUELLER in *Acrostichum* in 1870. UNDERWOOD places *T. brightiae* (as *Stenochlaena hügelii*) in *Stenochlaena sect. Lomariopsis*, remarking that *T. articulatum* belonged to a distinct genus *Arthrobotrya*. In his early work on Philippine ferns, COPELAND transferred *T. articulatum* to the genus *Lomagramma* because of its similarity to *L. polyphylla* (with which it had been associated by DIELS, who placed the simple pinnate *Lomagramma* species in *Gymnopteris*). In Genera Filicum (1947) COPELAND revived the genus *Arthrobotrya*; but he avoided consideration of the species *T. brightiae*, which has always simple acrophylls. The only clearly definable character distinguishing the two sections of *Teratophyllum*, as here presented, is the polyseriate or biseriate arrangement of fronds on the upper surface of the rhizome, with accompanying difference of vascular structure; this does not appear to me to warrant generic separation of the two.

10. Teratophyllum articulatum (J.SM. *ex* FÉE) METT. *ex* KUHN, Ann. Mus. Bot. Lugd.-Bat. 4 (1869) 297; HOLTTUM, Gard. Bull. S. S. 9 (1938) 356. — *Polybotrya articulata* J.SM. *ex* FÉE, Hist. Acrost. (1845) 74, t. 37; CHRIST, Farnkr. Erde (1897) 42, f. 101; DIELS in E. & P. Nat. Pfl. Fam. 1, 4 (1899) 198; COPEL. Polypod. Philip. (1905) 40; HOLTTUM, Blumea 14 (1966) 217. — *Acrostichum* (*sect. Polybotrya*) *articulatum* HOOK. Spec. Fil. 5 (1864) 247. — *Arthrobotrya articulata* J.SM. Hist. Fil. (1875) 141; COPEL. Gen. Fil. (1947) 118; Philip. J. Sc. 78 (1949) 401; Fern Fl. Philip. (1960) 272. — *Lomagramma articulata* COPEL. Philip. J. Sc. 3 (1908) Bot. 32; v.A.v.R. Handb. Suppl. (1917) 437. — Type: CUMING 296, Luzon (BM, GH, K, P).

Lomagramma bipinnata COPEL. Philip. J. Sc. 11 (1916) Bot. 41; v.A.v.R. Handb. Suppl. (1917) 438. — Type: RAMOS BS 17515, Samar (MICH). — **Fig. 8.**

Youngest stage with simply pinnate fronds to 9 cm long with deeply crenate articulate pinnae 8 by 4–5 mm, apex of frond a narrow lobed lamina not articulate; next stage with basal pinnae pinnate and in some cases deflexed across rhizome, upper simple pinnae to 22 by 11 mm, pinnules of basal pinnae to 6 by 4 mm; later fully bipinnate fronds 2-ranked on slender rhizome are like acrophylls but smaller. *Adult rhizome* 7–8 mm or more wide, smooth. *Sterile acrophylls* with stipes 10–20 cm, lamina to 60 cm long, bipinnate; pinnae 15–24 cm long, articulate to rachis, pinnate with to 20 or more pairs of articulate pinnules which grade into the small widely-spaced lobes of a narrow apical lamina; pinna-rachis winged throughout; pinnules sessile or nearly so, base very asymmetric, narrowly cuneate basiscopically, very broadly cuneate and usually with a well-developed auricle acroscopically, edges crenate, apex rounded, largest pinnules 15–25 mm long, 6–8 mm wide above auricle; brown bullate scales on lower surface of costa. *Fertile fronds* somewhat smaller than sterile; pinnules distinctly stalked, 7–15 mm long, *c.* 2 mm wide when dry, distinctly auricled.

Distr. *Malesia:* Celebes (SW. & NE.), Moluccas (Ceram, Halmahera), Philippines (Luzon, Leyte, Samar, Mindanao), New Guinea; Solomon Islands.

Notes. This species is distinguished from *T. wilkesianum* (New Caledonia, Fiji, Samoa, Tahiti) by the auricled acroscopic base of its pinnules, and by the complete absence of simply pinnate acrophylls; also apparently by the brown bullate scales of the lower surface of pinnules.

Two SARASIN specimens from N. Celebes match *T. wilkesianum* from New Caledonia very closely in shape of leaflets, but they have the scales characteristic of *T. articulatum*. It seems possible that these specimens represent a distinct local form of the species. COPELAND (1960: 273) refers to a specimen of his own from Mindanao which resembles *T. wilkesianum*; this has rather small fronds with deeply incised small leaflets which are very asymmetric at the base and seem to me much less like *T. wilkesianum* than the Celebes specimens.

4. LOMAGRAMMA

J.SM. in Hook. J. Bot. 3 (1841) 402, *nom. nud.*; in Hook. Gen. Fil. (1842) t. 98; BEDD. Handb. Ferns Br. India Suppl. (1892) 105; C.CHR. Ind. Fil. Suppl. 1 (1913) 49 (*p.p.*), 118; v.A.v.R. Handb. Suppl. (1917) 436, *excl. L. articulata et bipinnata*; COPEL. Univ. Cal. Publ. Bot. 16 (1929) 76, *excl. L. articulata*; HOLTTUM, Gard. Bull. S. S. 9 (1937) 190–221; Rev. Fl. Mal. 2 (1954) 477; COPEL. Fern Fl. Philip.

(1960) 273–275; HOLTTUM, Blumea 14 (1966) 221–223. — *Leptochilus* KAULF. *p.p.* BL. En. Pl. Jav. (1828) 206; C.CHR. Bot. Tidsskr. 26 (1904) 283; Ind. Fil. (1905) xxvi; v.A.v.R. Handb. (1908) 746. — *Cheilolepton* FÉE, Hist. Acrost. (1845) 19. — *Neurocallis* FÉE *p.p.* PRESL, Epim. Bot. (1851) 177. — *Chorizopteris* MOORE, Gard. Chron. Agr. Gaz. (1855) 854. — *Neurocallis sect. Cheilolepton* MOORE, Ind. Fil. (1857) xix. — *Acrostichum sect. Chrysodium* (FÉE) HOOK. Spec. Fil. 5 (1864) 268, *p.p.*; BAKER, Syn. Fil. (1868) 423. — *Polybotrya* HUMB. & BONPL. *sect. Lomagramma* KUHN, Ann. Mus. Bot. Lugd.-Bat. 4 (1869) 295. — *Gymnopteris* BERNH. *p.p.* DIELS in E. & P. Nat. Pfl. Fam. 1, 4 (1899) 198. — **Fig. 9–14.**

Rhizome of adult plant climbing tree-trunks, broad, bearing 3–5 rows of fronds on dorsal surface (except *L. brassii* which has 2 rows), 3 or more fronds often attached close together, such groups rather widely separated; young parts of rhizome and young fronds densely scaly; scales peltate, smaller ones always clathrate, larger ones often with a central or basal area of uniformly thin-walled cells with darker contents; vascular system as in *Lomariopsis*. *Stipes* gradually decurrent at their bases to ridges on rhizome, the pale linear aerophore on each side of a stipe decurrent also. *Young plants* with slender rhizome bearing only 2 longitudinal rows of fronds, creeping on rocks or on the ground; fronds widely separated, of distinctive form (bathyphylls). *Fronds* simply pinnate (bipinnate in *L. polyphylla* BRACK., New Hebrides to Fiji, also recently discovered in *L. cordipinna* HOLTTUM in Fiji) with all pinnae, apical one included, jointed to rachis; scales on fronds clathrate, smaller ones bullate at base; veins forming a uniform network of 3 or more rows of oblique areoles without included veinlets and without main veins; edges of sterile pinnae entire or crenate. *Fertile fronds* with pinnae narrower than sterile, covered beneath with sporangia, venation as sterile but areoles fewer; slender-stalked paraphyses present, about as long as sporangia, their apices dilated, irregular in shape, formed of 8–10 cells with thick lateral walls as small scales on other parts of plant. *Spores* lacking perispore.

Type species: *L. pteroides* J.SM.

Distribution. Assam to S. China and Thailand; throughout Malesia except the eastern Lesser Sunda Is.; Solomon and New Hebrides to Tahiti; about 18 *spp.* (one species in tropical America has been included by CHING, but its status is doubtful,; see p. 278, 289).

Ecology. In all cases where young plants have been observed, they grow on wet rocky banks of small streams in high forest, at altitudes from sea level to 1500 m. Their slender rhizomes, bearing erect fronds, are wide-creeping, extending into the forest away from the stream until they meet tree-trunks, up which they climb vertically, attached by roots, to 10 m or more (fig. 9), developing a much thicker rhizome and larger horizontal or drooping fronds. Fertile fronds are produced on the upper parts of climbing rhizomes, probably in response to drier conditions; the only occasion on which I have seen fertile fronds on *L. sumatrana* in Malaya was on a plant which had recently been exposed by felling of neighbouring trees. *L. sinuata* in New Guinea tolerates more exposed conditions than *L. sumatrana* and can continue to grow after partial clearing of forest. Spores are probably short-lived; this may limit their dispersal range.

Vegetative morphology. In morphology and anatomy of rhizome *Lomagramma* is closely similar to *Lomariopsis*, but scales are wholly or partly clathrate. Young plants of all species have simply pinnate fronds with jointed pinnae and a lobed apical lamina continuous with the rachis. Sooner or later fronds are produced in which this lobed apex is aborted (a rudiment can sometimes be seen) and its place taken by a pinna which is jointed at its base. In some species this change takes place only when the plant is large enough to produce fronds with many pinnae (see special key below); in others the apical lamina is lacking from a much earlier stage when fronds have few pairs of pinnae. I have observed this distinction constantly between the two species in Malaya which I have seen many times in their native habitat. Unfortunately young stages have not been well collected for most species, or collections have consisted only of young stages without association of the adult stage. The venation of sterile acrophyll pinnae is very constant in all cases; that of fertile pinnae has small areoles, in number varying with width of pinnae. There is not a great range in shape and size of pinnae, whether sterile or fertile, and I have not found it possible to construct a complete key based only on sterile fronds (which are commonest in herbaria).

Gametophyte. See p. 258 *supra*.

Cytology. The only observations are by ROY and MANTON on root-tips of plants of *L. sinuata* and *L. melanolepis* sent by me from New Guinea and cultivated at Kew; both cases showed 2n = 82.

Taxonomy. JOHN SMITH based the genus on the peculiar condition of the fertile pinnae of *L. pteroides*, which have the sporangia confined to a marginal band with a narrow sterile area between this and the midrib, at least near the base of a pinna. In 1845 FÉE based the genus *Cheilolepton* on *L. lomarioides* (of which he published a good figure) but did not refer to *L. pteroides*, presumably because he thought it not to be acrostichoid, though J. SMITH had noted its possible identity with *L. lomarioides* (which he had not seen). MOORE also, in his scheme of classification (1857) placed *Lomagramma* (limited to *L. pteroides*) in a group of genera quite distinct from *Cheilolepton*, which latter he united with *Neurocallis* (a near ally of *Acrostichum s.str.*) because of similarity of venation. HOOKER (1864) stated that *L. pteroides* was only an abnormal form of *L. lomarioides*, and regarded specimens from Samoa (*L. cordipinna* HOLTTUM) as belonging to the same species. He placed *L. lomarioides* near *Acrostichum s.str.* and *Neurocallis* on account of their common characters of acrostichoid fertile pinnae and reticulate venation. KUHN (1869) placed *Lomagramma* as a section of *Polybotrya*. In his last work BEDDOME (1892) recognized *Lomagramma* once more as a distinct genus, and described a new species (*L. perakensis*); but DIELS (1899) relegated it again to a confused mixture of acrostichoid ferns of very diverse affinity in *Gymnopteris*. CHRISTENSEN (1904) placed *Lomagramma* as a section of *Leptochilus* (another section being *Bolbitis*) but later recognized it as a distinct genus.

As noted in the introductory statement on this group of genera, I regard *Lomagramma* as closely related to *Bolbitis*. *Lomagramma* differs from *Bolbitis* constantly in Malesia in the following characters: high-climbing rhizome, articulate pinnae, reticulate venation without main veins or included free veinlets and thin-walled spores lacking perispore. In tropical America there is a species of *Bolbitis* which is very near *Lomagramma* in venation, *B. serratifolia* (KAULF.) CHING. The species originally named *Polypodium guianense* AUBL. has been placed in *Lomagramma* by CHING and in *Bolbitis* by KRAMER. It has *Lomagramma*-like bathyphylls, a high-climbing rhizome and articulated pinnae. In my view it is not closely related to Malesian *Lomagramma* (see p. 289). There is considerable variation in the pattern of venation in *Bolbitis*, and in Malesia also are species which have a reticulate venation lacking free included veinlets, though none lack main lateral veins. Bathyphyll pinnae of *Lomagramma* have a toothed margin much as some *Bolbitis spp*. If one has a small detached bathyphyll from a young plant of *Lomagramma*, the only character by which one can be sure it is not *Bolbitis* is the jointed pinnae.

COPELAND wrote (Fern Fl. Philip. 1960, 275) "at present it does not seem to me quite impossible that our specimens (of *Lomagramma*) represent a single widely variable species". I am sure that distinct species exist, but admit that in New Guinea I have found their delimitation difficult. More field work is necessary before a better arrangement can be established; information on all stages of development, gained separately in individual localities, is needed. It is possible that hybrids exist, as in *Bolbitis*.

Keys. As noted above, the most characteristic parts of a *Lomagramma* species are often the bathyphylls and the fertile fronds. I find it impossible to construct a satisfactory key which does not include these characters, and they are used in the main key which follows. Incomplete keys, based only on one of the three different kinds of fronds, are also given, as a help to the identification of incomplete specimens.

KEY TO THE SPECIES

1. Mature plants with broad rhizomes bearing 3 or more rows of fronds; sterile acrophyll pinnae not toothed throughout.
 2. Sterile acrophyll pinnae very firm, veins indistinct, not prominent on upper surface.
  3. Sterile acrophyll and bathyphyll pinnae entire or at most sinuate towards apices; fertile pinnae to 20 cm long.
   4. Sterile acrophyll pinnae to $12^1/_2$ by $1^1/_2$ cm, base broadly cuneate to truncate and sometimes slightly auricled on acroscopic side; fertile pinnae to 2 mm wide . . . . . **1. L. lomarioides**
   4. Sterile acrophyll pinnae to 25 by $2^1/_2$ cm, base narrowly cuneate; fertile pinnae 3–5 mm wide **2. L. perakensis**
  3. Sterile acrophyll pinnae distinctly toothed towards apex; fertile pinnae to 10 cm long.
   5. Fertile pinnae 3 mm wide, stalks to 5 mm long . . . . . **3. L. merrillii**
   5. Fertile pinnae 8 mm wide, sessile . . . . . **4. L. novoguineensis**
 2. Sterile acrophyll pinnae with veins distinct and ± prominent on upper surface.
  6. Fertile pinnae $4^1/_2$ by 0.8 cm with rounded apices; sterile pinnae 1.3 cm wide, toothed towards apices . . . . . **4. L. novoguineensis**
  6. Fertile pinnae narrower or much longer; sterile wider or with entire edges.
   7. Sterile acrophyll pinnae to 8 mm wide, entire . . . . . **5. L. angustipinna**
   7. Sterile acrophyll pinnae more than 1 cm wide, narrower ones often toothed towards apices.
    8. Bathyphylls with narrow lobed apical lamina continuous with rachis on fronds with 20 pairs of pinnae.
     9. Sterile acrophyll pinnae commonly 1.2–1.8 cm wide, broad and almost symmetrical at base; fertile pinnae dilated and partly sterile at base . . . . . **6. L. pteroides**
     9. Sterile acrophyll pinnae commonly 2 cm or more wide, asymmetric at base; fertile pinnae not dilated at base . . . . . **7. L. sumatrana**
    8. Bathyphylls with jointed apical pinna on fronds with few pairs of pinnae.

10. Base of lower sterile acrophyll pinnae broadly rounded or subcordate on both sides.
11. Pinnae firm and opaque, veins hardly prominent; scales on rhizome distinctly clathrate **8. L. brooksii**
11. Pinnae thin, veins prominent; scales on rhizome not clathrate except near their tips **9. L. leucolepsis**
10. Base of lower sterile acrophyll pinnae distinctly asymmetric, narrower on basiscopic side, acroscopic side usually broadly cuneate.
12. Fertile pinnae 5–8 mm wide; sterile pinnae 2–4 cm wide . . . . . **10. L. sinuata**
12. Fertile pinnae not over 4 mm wide, sterile mostly not over 2 cm wide.
13. Suprabasal sterile acrophyll pinnae rounded on basiscopic side at base **11. L. copelandii**
13. Suprabasal acrophyll pinnae narrowly cuneate on basiscopic side at base **12. L. melanolepis**
1. Mature plants with slender rhizome bearing 2 rows of fronds; sterile pinnae with edges strongly toothed throughout . . . . . **13. L. brassii**

KEY BASED ON STERILE ACROPHYLLS

1. Pinnae very firm and opaque, veins not or slightly prominent.
2. Pinnae to 26 cm long, base cuneate both sides . . . . . **2. L. perakensis**
2. Pinnae not over 15 cm long.
3. Pinnae entire.
4. Lower pinnae almost equally subcordate at base . . . . . **8. L. brooksii**
4. Lower pinnae unequal at base, acroscopically broadly truncate or slightly auricled **1. L. lomarioides**
3. Pinnae distinctly toothed towards apices . . . . . **3. L. merrillii** **4. L. novoguineensis**
1. Pinnae thinner, usually translucent when dry, veins always distinctly prominent.
5. Largest pinnae not over $1^1/_2$ cm wide.
6. Largest pinnae 10 by 0.8 cm, entire . . . . . **5. L. angustipinna**
6. Largest pinnae usually wider, strongly toothed. . . . . **13. L. brassii**
5. Largest pinnae wider.
7. Lower pinnae with basiscopic base broadly rounded to subcordate . . . . . **6. L. pteroides** **8. L. brooksii** **9. L. leucolepis**
7. Lower pinnae with basiscopic base cuneate or narrowly rounded.
8. Basiscopic base narrowly cuneate.
9. Pinnae 2–4 cm wide, to 20 cm long . . . . . **10. L. sinuata**
9. Pinnae rarely over 2 cm wide, shorter . . . . . **12. L. melanolepis**
8. Basiscopic base rounded . . . . . **7. L. sumatrana** **10. L. sinuata** *f.* **papuana** **11. L. copelandii**

KEY BASED ON BATHYPHYLLS ONLY

1. Apical lamina lobed and continuous with rachis on fronds with 15–20 pairs of pinnae.
2. Pinnae entire or with slightly sinuate edges . . . . . **1. L. lomarioides**
2. Pinnae distinctly toothed, at least towards apices.
3. Pinnae blunt-tipped, bluntly toothed, drying reddish . . . . . **6. L. pteroides**
3. Pinnae acute (except youngest stages), acutely toothed, not drying reddish.
4. Pinnae falcate, toothed near apices only . . . . . **8. L. brooksii**
4. Pinnae toothed throughout.
5. Pinnae to 5 by 1.2 cm . . . . . **7. L. sumatrana**
5. Pinnae shorter and narrower . . . . . **4. L. novoguineensis**
1. Apical lamina replaced by a pinna jointed to rachis on fronds with few pairs of pinnae.
6. Pinnae entire or with slightly sinuate edges . . . . . **2. L. perakensis**
6. Pinnae distinctly toothed . . . . . **3. L. merrillii** **10. L. sinuata** **11. L. copelandii** **12. L. melanolepis** **13. L. brassii**

Bathyphyll characters not known . . . . . **5. L. angustipinna** **9. L. leucolepis**

1. Lomagramma lomarioides (BL.) J.SM. Hist. Fil. (1875) 143; BEDD. Handb. Suppl. (1892) 106, *p.p.*; v.A.v.R. Handb. Suppl. (1917) 438, *p.p.*; HOLTTUM, Gard. Bull. S. S. 9 (1937) 204, pl. 12, 13; BACKER & POSTH. Varenfl. Java (1939) 153; COPEL. Philip. J. Sc. 78 (1949) 401. — *Leptochilus lomarioides* BL. En. Pl. Jav. (1828) 206; v.A.v.R. Handb. (1908) 746, *p.p.* — *Cheilolepton blumeanum* FÉE, Hist. Acrost. (1845) 89, t. 51. — *Acrostichum blumeanum* (FÉE) HOOK. Spec. Fil. 5 (1864) 268, *p.p.*; BAKER, Syn. Fil. (1868) 423, *p.p.*; RACIB. Fl. Btzg 1 (1898) 55. — *Polybotrya lomarioides* (BL.) KUHN, Ann.

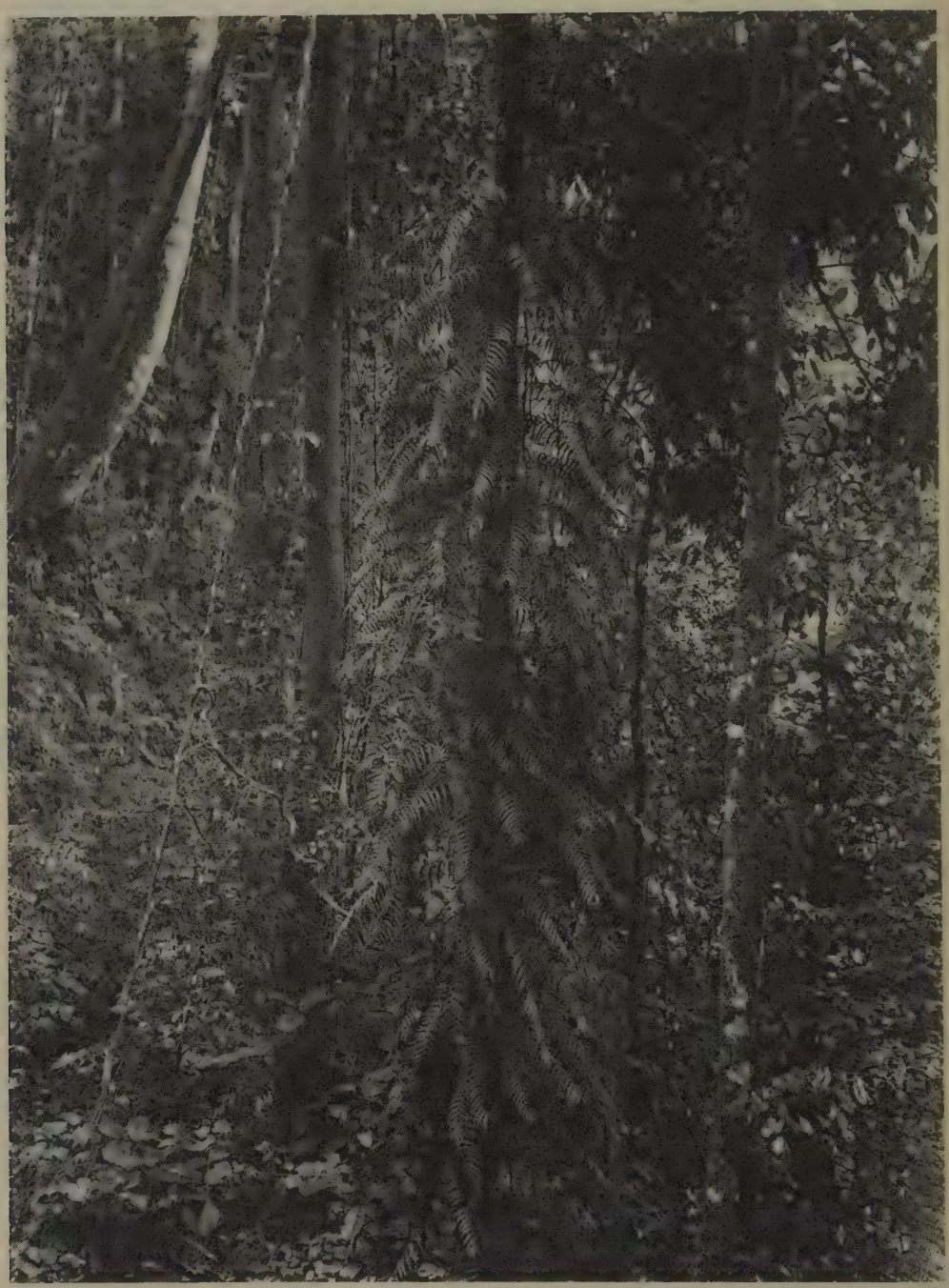

Fig. 9. *Lomagramma perakensis* BEDD. Acrophylls, on tree in forest at Cameron Highlands, Malaya (Photogr. R. E. HOLTTUM).

Mus. Bot. Lugd.-Bat. 4 (1869) 295. — Type: BLUME *s.n.*, Salak, Java (L).

L. abscondita v.A.v.R. Bull. Jard. Bot. Btzg II, 11 (1913) 16; Handb. Suppl. (1917) 439; Bull. Jard. Bot. Btzg III, 2 (1920) 159. — Type: RACIBORSKI *s.n.*, G. Salak (BO).

Rhizome scales thin, to 2 mm wide, strongly clathrate with brown cell-walls. *Bathyphylls* with pinnae to 25 pairs and apical lamina continuous with rachis; largest pinnae 5 by 1 cm, acroscopic base broadly cuneate to subcordate, basiscopic narrowly rounded, edges quite entire or slightly sinuate, apex acuminate, falcate, texture firm, veins hardly visible on upper surface, slightly prominent beneath. *Sterile acrophylls*: stipe to 20 cm, frond to 100 cm long, middle pinnae largest, lowest gradually reduced and more widely spaced; largest pinnae $12^1/_2$ by $1^1/_2$ cm, acroscopic base broadly cuneate to truncate and sometimes slightly auricled, basiscopic narrowly rounded; texture of old fronds very firm, veins hardly visible on upper surface, somewhat prominent below but rather broad; edges entire, often inrolled when dried, apex acuminate, falcate. *Fertile fronds:* pinnae sessile, to at least 18 cm long, 1–2 mm wide.

Distr. *Malesia:* Java, Lesser Sunda Is. (Bali).

Ecol. In forest at 750–1500 m.

Note. Bathyphylls have not often been collected; a good example is PALMER & BRYANT 1190, Tjibodas (US).

2. Lomagramma perakensis BEDD. Handb. Suppl. (1892) 107; v.A.v.R. Handb. Suppl. (1917) 439; HOLTTUM, Gard. Bull. S. S. 9 (1937) 210, pl. 16; Rev. Fl. Mal. 2 (1954) 478, f. 281. — *Leptochilus perakensis* (BEDD.) C.CHR. Ind. Fil. (1906) 387; v.A.v.R. Handb. (1908) 747. — Type: J. DAY *s.n.*, Perak (K). — **Fig. 9, 11f–g.**

Rhizome scales to 10 by $1^1/_2$ mm, dull brown, distinctly clathrate. *Bathyphylls* as small as 5 cm long with apical pinna jointed to rachis; stipes of largest bathyphylls 25 cm long, lamina *c.* 30 by 14 cm, pinnae 10–15 pairs oblique to rachis, sessile, edges entire or somewhat sinuous, not toothed, largest 7 by 1.2 cm, texture firm, veins not prominent. *Sterile acrophylls:* stipe to 40 cm, fronds to 125 cm long; pinnae oblique, largest 26 by $2^1/_2$ cm, subsessile, base rather narrowly unequally cuneate, edges slightly undulate, not toothed, apex falcate acuminate, texture very firm, veins hardly prominent on either surface. *Fertile fronds:* pinnae commonly to 20 cm long (largest seen 40 cm), 3–5 mm wide, on stalks 3–7 mm long.

Distr. *Malesia:* Sumatra, Malay Peninsula (north to Pattani in S. peninsular Thailand).

Ecol. In valleys in mountain forest, at 600–1400 m.

3. Lomagramma merrillii HOLTTUM, Gard. Bull. S. S. 9 (1937) 208, pl. 14; COPEL. Fern Fl. Philip. (1960) 274. — Type: MERRILL 8282, Mindanao, Zamboanga District (M, destroyed).

Bathyphylls: pinnae to *c.* 10 pairs, to 3 by 1.3 cm, acroscopic bases broadly, basiscopic narrowly, crenate, edges acutely toothed, apex acute; apical pinna largest and articulate, *c.* 6 by 1.4 cm. *Sterile acrophylls:* stipe to 15 cm, frond to 45 cm long; upper pinnae largest, *c.* 9 by 1.7 cm, falcate, base unequally cuneate, edges finely and irregularly toothed towards apex, subcoriaceous, veins not conspicuous. *Fertile pinnae* (seen only in immature condition) to 9 cm long, 3 mm wide, apex acute (?), stalks to 5 mm long.

Distr. *Malesia:* Philippines (Mindanao, Negros).

Ecol. In forest, at 1500 m.

Note. In 1937 I saw the type specimen from the Manila herbarium; this and the CLEMENS specimen also cited with the original description are now lost, and I do not know of any duplicates. The only post-war collections consist of bathyphylls.

4. Lomagramma novoguineensis (BRAUSE) C.CHR. Ind. Fil. Suppl. 3 (1934) 124; HOLTTUM, Gard. Bull. S. S. 9 (1937) 208, pl. 15; COPEL. Philip. J. Sc. 78 (1949) 401. — *Leptochilus novoguineensis* BRAUSE, Bot. Jahrb. 56 (1920) 117. — Type: LEDERMANN 9524, NE. New Guinea, Sepik River, Etappenberg, 850 m (B). — **Fig. 10a.**

Bathyphylls with apex continuous with rachis on fronds with many pinnae. *Sterile acrophylls:* pinnae to 11 by 1.3 cm, base subequally rounded to truncate (lowest pinnae with base narrower on basiscopic side), edges serrate towards apex, texture very firm, veins at most slightly prominent; bullate acuminate scales abundant on lower surface of costae and veins; apex of frond sometimes a narrow lobed lamina continuous with rachis. *Fertile pinnae* sessile, to $4^1/_2$ by 0.8 cm, apex rounded.

Distr. *Malesia:* New Guinea (W.–E.).

Note. Only two collections of acrophylls and fertile fronds are known, the second being from 50 m alt. in western New Guinea. A third collection, of bathyphylls only, may also represent this species (WOMERSLEY & MILLAR NGF 8571, Western Highlands of NE. New Guinea, 700 m). The fronds of this have up to 40 pairs of closely-placed pinnae below the narrow lobed apex; the larger pinnae resemble the upper pinnae of the type of *L. novoguineensis*. A poor specimen collected by CLEMENS (8083A, Sattelberg, 1000 m, B) may also represent this species, but fertile fronds are young, not fully expanded, so that the mature size of the pinnae cannot be judged.

5. Lomagramma angustipinna COPEL. Univ. Cal. Publ. Bot. 18 (1942) 222; Philip. J. Sc. 78 (1950) 402, pl. 6A. — Type: BRASS 13446, Idenburg River, W. New Guinea, 750 m (GH; dupl. in MICH).

Rhizome 7 mm wide, containing 4 meristeles besides the root-bearing ventral one; rhizome-scales 1–2 mm long, cell-walls very dark. *Sterile acrophylls:* stipe 14 cm; lamina 50 cm long with *c.* 30 pairs of pinnae, lower ones decreasing; middle pinnae $10^1/_2$ by 0.8 cm, falcate-acuminate, subsessile, base very narrowly cuneate on basiscopic side, broader on acroscopic, edges entire, texture thin, veins fine, distinct on both surfaces. *Fertile pinnae* to 9 cm by 3 mm, on stalks to 2 mm long.

Distr. *Malesia:* W. New Guinea. Known only from type collection.

6. Lomagramma pteroides J.SM. in Hook. J. Bot. 3 (1841) 402; *ibid.* 4 (1841) 152; in Hook. Gen. Fil. (1842) t. 98; COPEL. Philip. J. Sc. 1 (1906) Suppl. 166; v.A.v.R. Handb. Suppl. (1917) 438; HOLTTUM, Gard. Bull. S. S. 9 (1937) 213, pl. 13; COPEL. Fern Fl. Philip. (1960) 273. — *Acrostichum blumeanum*

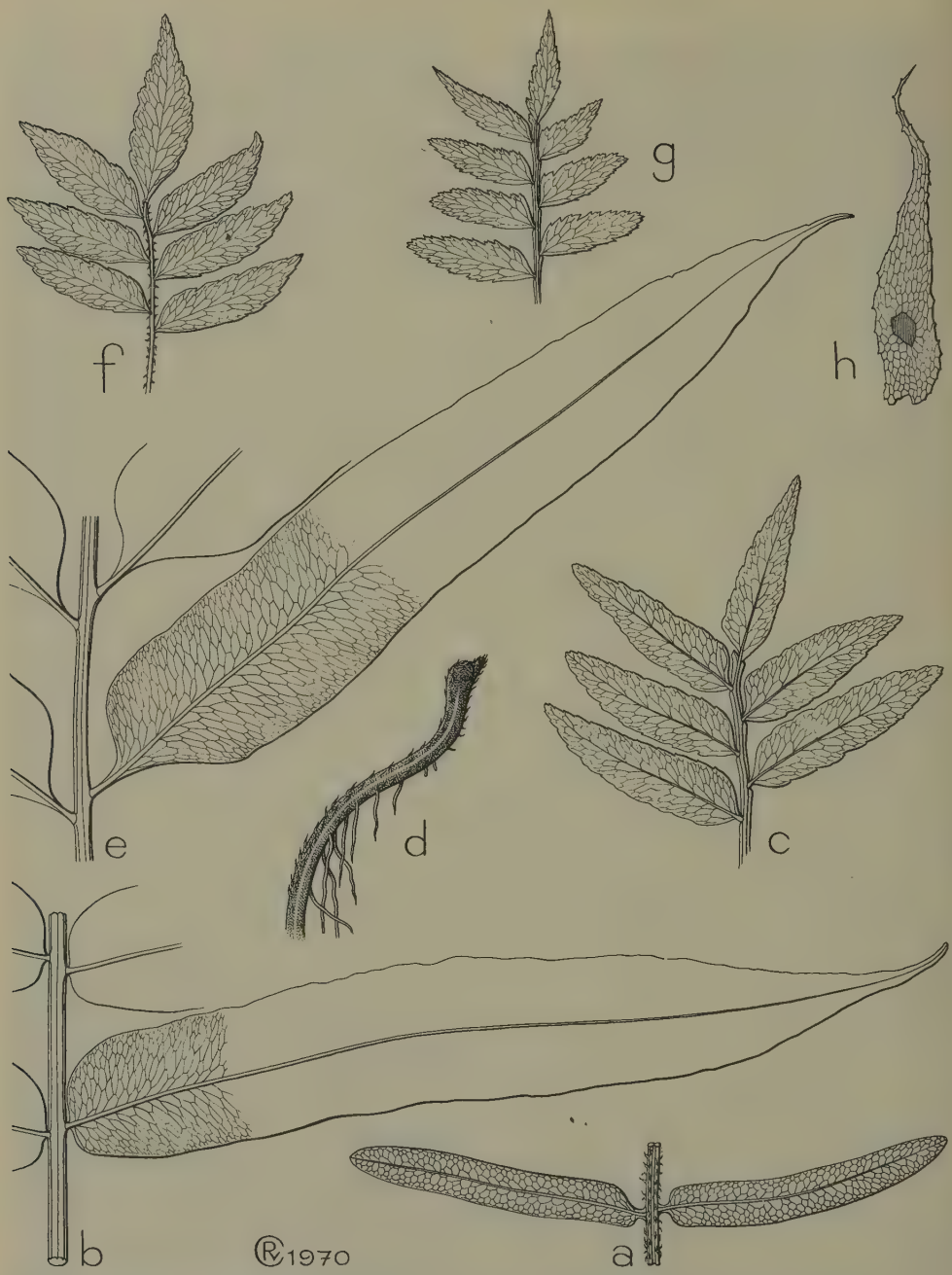

Fig. 10. *Lomagramma novoguineensis* (BRAUSE) C. CHR. *a*. Fertile pinnae, × $^2/_3$. — *L. sinuata* C. CHR. *f. papuana* C. CHR. *b*. Sterile acrophyll, *c*. apex of bathyphyll, *d*. rhizome of young plant, all × $^2/_3$. — *L. sinuata* C. CHR. Typical form, *e*. sterile acrophyll, *f*. apex of bathyphyll, both × $^2/_3$. — *L. melanolepis* v.A.v.R. *g*. Apex of bathyphyll, × $^2/_3$, *h*. scale from rhizome, × 20 (*a* DOCTERS VAN LEEUWEN 9616, *b–c* NGF 17699, *d*, *h* cult. Kew, origin Lae, *e* KOORDERS 23554, *f* BAKHUIZEN VAN DEN BRINK Jr 3664, *g* NGF 15892).

(FÉE) HOOK. Spec. Fil. 5 (1864) 268, *p.p.*; BAKER, Syn. Fil. (1869) 423, *p.p.* — *Polybotrya pteroides* (J.SM.) KUHN, Ann. Mus. Bot. Lugd.-Bat. 4 (1869) 295. — *Leptochilus lomarioides* BL. *var. pteroides* v.A.v.R. Handb. (1908) 746. — Type: CUMING 223, Luzon (BM; dupl. in K).

L. pteroides var. subcoriacea COPEL. Philip. J. Sc. 3 (1908) Bot. 32; v.A.v.R. Handb. Suppl. (1917) 439. — *L. subcoriacea* COPEL. Philip. J. Sc. 40 (1929) 308; Fern Fl. Philip. (1960) 274. — Type: COPELAND 1736, Mindanao (MICH; dupl. in B, BM, P).

L. pedicellata COPEL. Philip. J. Sc. 81 (1952) 23; Fern Fl. Philip. (1960) 275. — Type: EDAÑO PNH 531, Palawan (MICH).

L. cordata COPEL. Philip. J. Sc. 84 (1955) 162, t. 2. — Type: SULIT PNH 20277, Biliran (MICH). — **Fig. 11a–d.**

Bathyphylls with up to 28 pairs pinnae have lobed terminal lamina continuous with rachis; lower pinnae gradually reduced, lowest *c.* 7 by 3 mm, largest pinna $2^1/_2$ by 0.7 cm, base unequally cuneate (more narrowly on basiscopic side), edges crenulate with teeth 2–3 mm apart, apex often not acute, bases and apices of lower pinnae more rounded; stipe, rachis and costae rather densely scaly, scales dark; pinnae reddish when dry; veins strongly raised on both surfaces. *Sterile acrophylls:* stipes 20–30 cm, pinnae commonly 1.2–1.8 cm wide, 12–15 cm long (largest seen 22 by 2.2 cm), base slightly unequally subtruncate to subcordate, edges subentire and parallel, apex acuminate and somewhat falcate, irregularly sinuate or somewhat toothed, uppermost pinnae gradually smaller with less truncate base and more toothed apex, lowest pinnae not much reduced but often with cordate

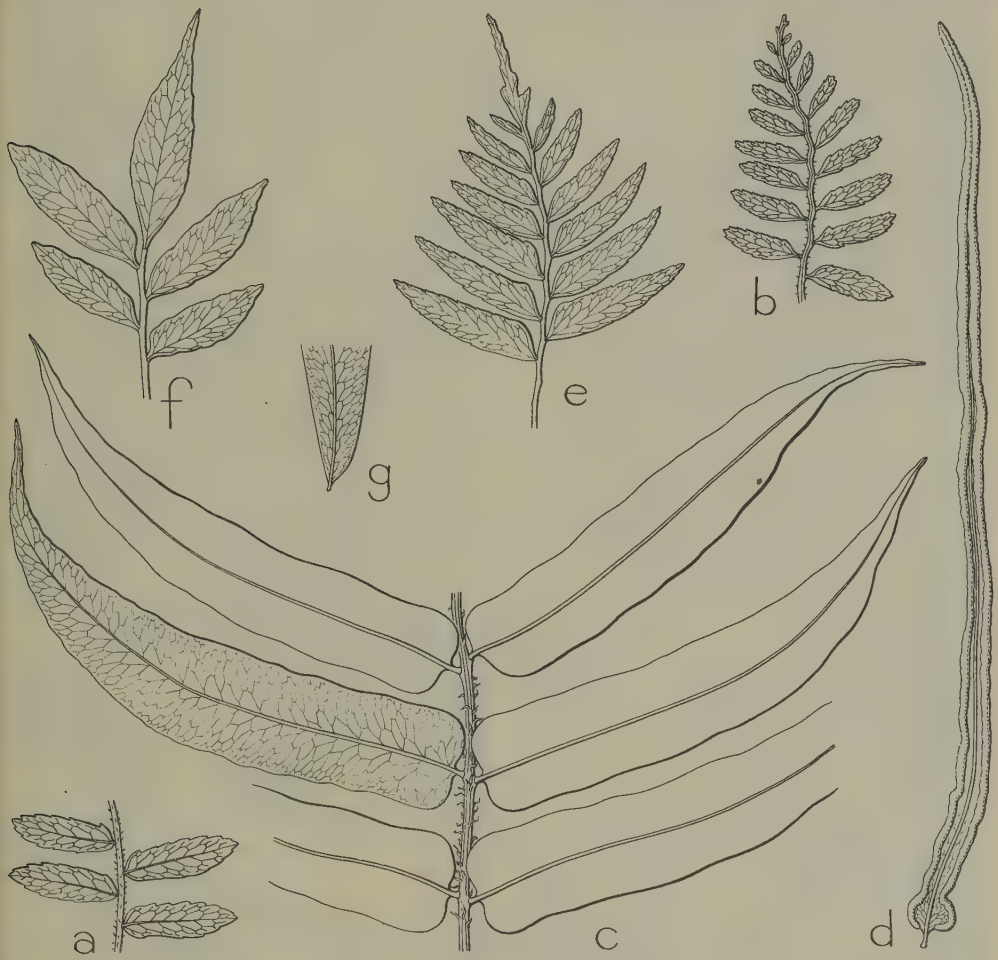

Fig. 11. *Lomagramma pteroides* J. SM. *a.* Middle pinnae of bathyphyll, *b.* apex of bathyphyll, *c.* sterile acrophyll, *d.* fertile pinna, all × $^2/_3$. — *L. sumatrana* v.A.v.R. *e.* Apex of bathyphyll, × $^2/_3$. — *L. perakensis* BEDD. *f.* Apex of bathyphyll, *g.* base of pinna of acrophyll, both × $^2/_3$ (*a–b* EDAÑO 476, *c–d* ELMER 9068, *e* MATTHEW *s.n.*, Jan. 1907, *f–g* HOLTTUM 24994).

Fig. 12. *Lomagramma sinuata* C. CHR. Transition from bathyphylls (centre) to acrophylls (base, left & right), Cult. R.B.G. Kew, origin NE. New Guinea (Photogr. R. VAN CREVEL).

base; texture thin, colour often reddish when dry; veins slightly prominent, areoles rather small, dark scales rather abundant. *Fertile fronds:* pinnae commonly to 20 cm long, base unequally cuneate, widening suddenly from a winged stalk to 10 mm long; base of pinna 7–10 mm wide, only the edges fertile, upper part gradually narrowed, distal half sometimes covered with sporangia but often with a narrow sterile band each side of midrib.

Distr. *Malesia:* Philippines (Luzon, Palawan, Negros, Panay, Mindoro, Mindanao).

Ecol. Apparently in lowland forest and to *c.* 1000 m (records few).

Notes. I have not seen the type of *L. cordata* COPEL. The photographic illustration shows a complete frond sterile at the base, fertile in distal parts. The sterile pinnae are only 7 mm wide, but on such a frond would probably not be normal. The fertile pinnae are rather long-stalked even to the apex of the frond (stalks are evidently 4–6 mm long, not 4–6 cm as in the printed description) where stalks are usually shorter.

M. G. PRICE has collected on Mt Makiling bathyphylls of this species in which the lower pinnae are gradually decrescent, but the lowest are elongate and deeply lobed so as to be almost pinnate.

7. Lomagramma sumatrana v.A.v.R. Bull. Jard. Bot. Btzg III, 2 (1920) 158; HOLTTUM, Gard. Bull. S. S. 9 (1937) 217, pl. 16; Rev. Fl. Mal. 2 (1954) 477, f. 280. — Type: LÖRZING 5564, Sumatra, Sibolangit (BO; dupl. in P, SING). — **Fig. 11e.**

Bathyphylls: stipes 3–10 cm long; lamina to 40 by 9 cm; pinnae 20–30 pairs, lowest rather reduced and deflexed, upper gradually smaller, uppermost grading into lobes of frond-apex which is not pinna-like not jointed; middle pinnae to 5 by 1.2 cm, at right angles to rachis, acroscopic base broadly subtruncate to subauriculate, basiscopic narrower, rounded, sides almost parallel for $^2/_3$ of length, then tapering to acute apex; edges shallowly crenate with 1–2 teeth at distal end of each crenation; texture thin, veins slender, prominent. *Sterile acrophylls:* stipes to 20 cm, frond to at least 90 cm long; lowest pinnae somewhat reduced and more distant, uppermost gradually smaller; middle pinnae to 18 by $2^1/_2$ cm, sessile or subsessile, acroscopic base broadly cuneate, basiscopic narrower and rounded to cuneate; edges usually with a few irregular teeth towards acuminate apex; texture thin, veins conspicuous. *Fertile pinnae* to 15 cm by 5 mm, on stalks to 2 mm, upper ones gradually reduced, uppermost *c.* 4 cm long.

Distr. *Malesia:* N. Sumatra, Malay Peninsula.

Ecol. Near rocky streams in forest, 0–500 m.

Note. Acrophyll pinnae of this species are very similar in shape to those of *L. sinuata*, though never so large; bathyphylls show a constant difference in all cases observed.

8. Lomagramma brooksii COPEL. Philip. J. Sc. 3 (1908) Bot. 345; *ibid.* 7 (1912) Bot. 60; v.A.v.R. Handb. Suppl. (1917) 439; HOLTTUM, Gard. Bull. S. S. 9 (1937) 199, pl. 8 (by error as *L. borneensis*). — Type: HEWITT & BROOKS, Bongo Mt, Sarawak (MICH).

Bathyphylls on young plants, with apical lamina continuous with rachis, to 20 cm long with 12–15 pairs pinnae; larger bathyphylls with apical pinna articulate; pinnae of youngest plants with rounded apex, of larger ones acute; acroscopic base broadly subtruncate and sometimes slightly auricled, basiscopic much narrower, rounded; edges toothed only towards apices; texture thin, veins distinct and slightly raised on both surfaces. *Sterile acrophylls:* stipe short (often only 4 cm); fronds to 75 cm long; middle pinnae at right angles to rachis, sessile, to 15 by 2 cm, basiscopic base rounded to subcordate, a little narrower than subtruncate acroscopic base; edges entire, sometimes sinuate towards apices; texture thin but very firm, veins slightly raised; lower pinnae slightly stalked, their bases symmetrical and subcordate. *Fertile pinnae* to 15 cm by 4 mm, more commonly smaller, on winged stalks to 2 mm.

Distr. *Malesia:* N. Borneo (Sarawak), North & Central Celebes, Philippines (Luzon, Palawan).

Ecol. Near streams in forest, at 300–1500 m.

Note. The North Celebes specimen (POSTHUMUS 2335) has bathyphylls with 20 pairs of pinnae and still a narrow lobed apical lamina continuous with the rachis. Central Celebes specimens (SARASIN 953) have fronds not completely expanded.

9. Lomagramma leucolepis HOLTTUM, Blumea 14 (1966) 224. — Type: BRASS 12950, W. New Guinea, Idenburg River (L; dupl. in BM, BO, GH, MICH).

Rhizome 12 mm ∅, containing 3 meristeles besides ventral root-bearing one; scales rather light brown, not clathrate, to $1^1/_2$ mm wide. *Sterile acrophylls:* stipes 12 cm long, sparsely covered with small pale brown scales, only the smallest clathrate; frond 75 cm long, rachis bearing scales with bullate bases; pinnae to 14 by 2 cm, sessile, basiscopic base subcordate or rounded, acroscopic broader and rounded in lower pinnae, broadly cuneate in upper, apex acuminate, edges very broadly crenate in distal $^1/_3$; veins fine, distinctly raised on both surfaces; scales rather abundant on midrib and veins of lower surface, bullate-acuminate. *Fertile pinnae* of type mostly broken, largest intact one (near base of frond) 7 cm long (in herb. MICH to $10^1/_2$ cm), 3–5 mm wide, subsessile, base rounded, slightly narrowed towards blunt apex.

Distr. *Malesia:* W. New Guinea. Only known from the type.

Ecol. Steep slope in rain-forest, at 1200 m, locally common.

10. Lomagramma sinuata C.CHR. Svensk Bot. Tidskr. 16 (1922) 98, f. 5; HOLTTUM, Gard. Bull. S. S. 9 (1937) 215; BACKER & POSTH. Varenfl. Java (1939) 153; COPEL. Philip. J. Sc. 78 (1949) 401; HOLTTUM, Blumea 14 (1966) 222. — *L. sinuata f. papuana* C.CHR. Brittonia 2 (1937) 302. — Type: KAUDERN 73, N. Celebes (BM; dupl. in BO).

Leptochilus cuneatus R.BONAP. Notes Pterid. 14 (1923) 453. — Type: BROOKS 467, Bencoolen, Sumatra (P; dupl. in BM).

Lomagramma sp. HOLTTUM, Gard. Bull. S. S. 9 (1937) 219. — **Fig. 10b–f, 12.**

Rhizome often bearing 3–5 fronds close together at wide intervals; scales on rhizome-apex distinctly clathrate with very dark cell-walls, edges paler and sometimes fringed. *Bathyphylls:* fronds with 10–12 pairs of pinnae have apical pinnae jointed to rachis; rachis distinctly winged; middle pinnae to 9 by

Fig. 13. *Lomagramma melanolepis* v.A.v.R. Young plant, bathyphylls stage. Cult. R.B.G. Kew, origin NE. New Guinea (Photogr. R. VAN CREVEL).

2 cm with broadly cuneate acroscopic base and narrowly cuneate or slightly rounded basiscopic, edges shallowly crenately lobed (more deeply towards pinna-apex) with irregular small teeth on the crenations, apex rounded to bluntly pointed. *Sterile acrophylls* to 100 cm long with many pinnae; middle pinnae 11 by 2 cm to 20 by 4 cm, more or less stalked, acroscopic base broadly cuneate, its edge forming a distinct S-curve, basiscopic base narrowly cuneate (sometimes rather rounded in New Guinea), edges almost entire on larger fronds, slightly and irregularly toothed towards apex on smaller ones, texture thin, veins fine and distinctly raised on both surfaces. *Fertile fronds:* pinnae 10–25 cm long, 5–8 mm wide, on stalks 2–8 mm long.

Distr. *Malesia:* S. Sumatra, Java, Lesser Sunda Is. (Bali), Borneo, Celebes, Moluccas (Batjan), New Guinea; Solomon Is.

Ecol. In forest near streams, up to 750 m.

Notes. The type, and some other specimens from Celebes and Java, have pinna-stalks 5 mm or more long, narrowly winged on the acroscopic side (fig. 10e). Most specimens from Java and New Guinea have pinnae almost sessile but do not differ significantly in other ways, though some in New Guinea (*f. papuana*, fig. 10b) are more rounded basiscopically.

In 1937 (*l.c.*, p. 219) I thought that most specimens now ascribed to this species from Java probably represented a distinct species, but the specimens in the Bogor herbarium on which I based this opinion did not include sterile acrophylls from fully mature plants nor fertile fronds. In the Rijksherbarium at Leiden are excellent specimens of large sterile acrophylls with quite entire pinnae 3 cm wide, and fertile fronds with pinnae 6–7 mm wide; these are indistinguishable from typical *L. sinuata* except that the sterile pinnae are shorter-stalked. Bathyphylls from West Java have more deeply crenate pinnae with a more acute apex than pinnae of fronds of a comparable size attributed to *L. sinuata* in East Java; this may be due to environmental factors. The species is probably now rare in Java owing to destruction of lowland forest.

11. Lomagramma copelandii HOLTTUM, Gard. Bull. S. S. 9 (1937) 201, pl. 9, 10; COPEL. Fern Fl. Philip. (1960) 274. — Type: RAMOS & EDAÑO BS 28826, Mt Binuang, Prov. Tayabas, Luzon (BO; original at MAN lost).

L. pteroides var. negrosensis COPEL. in Elmer, Leafl. Philip. Bot. 2 (1908) 393; v.A.v.R. Handb. Suppl. (1917) 438. — Type: ELMER 10175, Negros (MICH).

Bathyphylls to 15 cm long with apical lamina continuous with rachis, larger ones with jointed small terminal pinna; pinnae to *c.* 15 pairs, largest $6^1/_2$ by 1.8 cm, acroscopic side broadly cuneate at base, basiscopic rounded and narrower, edges crenately lobed (lobes *c.* 5 mm) each lobe with 2–4 short teeth, largest pinnae toothed only towards acute apex, on smaller fronds apex blunt. *Sterile acrophylls:* stipe 15–25 cm; pinnae to 18 by 3 cm, sessile, acroscopic base of middle pinnae broadly cuneate to subtruncate, basiscopic rounded, edges slightly undulate, not toothed, apex acuminate, texture thin, veins conspicuous. *Fertile fronds:* pinnae to 20 cm long and 4 mm wide, sessile, base not dilated, whole lower surface except costa soriferous, areoles long and narrow.

Distr. *Malesia:* Philippines (Luzon, Catanduanes, Samar, Bohol, Negros, Mindanao).

Ecol. Apparently in lowland forest, altitudes not recorded.

Note. ELMER distributed, with at least some specimens of his collection *no* 16919, fertile pinnae of *Lomariopsis subtrifoliata* with sterile fronds of *Lomagramma copelandii*.

12. Lomagramma melanolepis v.A.v.R. Bull. Jard. Bot. Btzg III, 5 (1922) 212; HOLTTUM, Gard. Bull. S. S. 9 (1937) 208. — Type: BEGUIN 1114, Ternate (BO). — **Fig. 10g–h, 13, 14.**

Rhizome-scales 4–5 mm long, narrow, dark-clathrate with paler edges bearing some hairs; fronds often 3 close together. *Bathyphylls* (New Guinea) with closely-placed strongly toothed pinnae which are commonly *c.* 20 by 6 mm; apical pinna jointed to rachis on fronds with 12 pairs of pinnae. *Sterile acrophylls:* middle pinnae subsessile, to 12 by 2 cm, rather thin with distinctly raised veins, base rather broadly cuneate on acroscopic side, narrower and cuneate to narrowly rounded on basiscopic, edges entire or somewhat toothed towards apex. *Fertile fronds:* pinnae to 9 cm long and 2–3 mm wide, usually stalked.

Distr. *Malesia:* Moluccas (Ternate, Halmaheira), New Guinea, d'Entrecasteaux Is.

Ecol. In lowland forest, to 900 m.

Note. This is very like *L. sinuata*, but has consistently smaller pinnae of both bathyphylls and acrophylls and narrower fertile pinnae. I have included numerous New Guinea collections which differ from the type in the very narrowly cuneate basiscopic base of sterile pinnae. If further collections from the Moluccas should indicate that the New Guinea plants are distinct, the latter will need a new name.

13. Lomagramma brassii HOLTTUM, Blumea 14 (1966) 224. — Type: BRASS 24947, Goodenough I. (A).

Rhizome of adult plant 3–4 mm ∅, carrying fronds in two longitudinal rows; scales to 3 by $^1/_2$ mm, clathrate with brown cell-walls. *Sterile fronds:* stipe 3–6 cm long; lamina to 25 cm long with 12–15 pairs of pinnae, apical one largest and jointed to rachis; a few basal pinnae gradually smaller and with rounded apices; middle pinnae of type to $4^1/_2$ by 0.9 cm, of another collection 8 by 1.1 cm, sessile, basiscopic base narrowly cuneate, acroscopic broadly so, apex tapered and acute, edges with an acute falcate tooth corresponding to each costal areole and irregular smaller intermediate teeth; veins forming one series of costal areoles and in the largest pinnae an irregular second series; small dark bullate-acuminate strongly clathrate scales abundant on lower surface of costa and a few on veins. *Fertile fronds:* lamina *c.* 15 cm long; pinnae 2 mm wide, largest $2^1/_2$–$5^1/_2$ cm long, apex rounded, stalks 1 mm long.

Distr. *Malesia:* New Guinea (Goodenough I.). Two collections.

Ecol. In transitional oak-rain-forest, 900 m, climbing to 2–3 m.

Note. This is very near *L. melanolepis*, but smaller, and the only clear difference is in the

Fig. 14. *Lomagramma melanolepis* v.A.v.R. Part of plant shown in fig. 13; bathyphyll with winged rachis and toothed pinnae which are all articulate (Photogr. R. VAN CREVEL).

slender rhizome of the adult stage of the plant. In view of the clear difference between *L. sinuata* and *L. melanolepis*, which is mainly one of size (and which is maintained by plants growing side by side in cultivation at Kew) I think it probable that *L. brassii* is a distinct species.

A plant in cultivation at Kew (accession *n.* 020/74-00297, J. R. WOODHAMS), collected in the vicinity of Sogere in Papua climbing on the trunk of a dead *Cyathea*, agrees well with the above description except that the pinnae are smaller: sterile to $3^1/_2$ by 1.1 cm, fertile *c.* $1^1/_2$ by 0.3 cm. The small size may be due to conditions of cultivation; at least the plant confirms that the fertile condition can be attained by quite small plants, a condition otherwise unknown in the genus.

Doubtful species

Lomagramma guianensis (AUBL.) CHING, Amer. Fern J. 22 (1932) 17. — *Polypodium guianense* AUBL. Hist. Pl. Guian. 2 (1775) 962.

This species occurs in the Greater Antilles and in South America from Guiana to southern Brazil. In habit, frond-form, venation and articulated pinnae it agrees closely with species of *Lomagramma* in Malesia and the Pacific. It differs in the following characters: acrophyll frond-apex deltoid, lobed, not pinna-like (as in bathyphylls of Malesian species); small scales not bullate; paraphyses hair-like with a glandular apical cell; spores with folded perispore as in *Bolbitis* and *Lomariopsis*. The paraphyses are much like the hairs on the margins of small scales of *Lomariopsis*, but scales on rhizome and frond are clathrate as in *Bolbitis* and *Lomagramma*. CHING included this species in *Lomagramma*, but its differences from Malesian species are such that I doubt its genetic unity with them; an independent origin in South America seems to me more probable, in which case a new genus might be established for it.

Lomagramma sorbifolia (WILLD.) CHING, Lingn. Sc. J. 12 (1933) 566; HOLTTUM, Gard. Bull. S. S. 9 (1937) 220. — *Aspidium sorbifolium* WILLD. Spec. Pl. 5 (1810) 23. — *Nephrodium sorbifolium* (WILLD.) PRESL, Rel. Haenk. (1825) 31, *nomen tantum*; HOLTTUM, Novit. Inst. Bot. Univ. Carol. Prag. 1968 (1969) 17.

WILLDENOW's type is a detached bathyphyll; the only locality given is "Ind. or." When CHING regarded WILLDENOW's specimen as conspecific with *L. lomarioides* (BL.) J.SM. he took a very broad view of the latter species; certainly WILLDENOW's specimen is quite unlike bathyphylls of *L. lomarioides* as described in the present work. It seems to me probable that WILLDENOW's specimen represents the same species as the type of *L. matthewii* (CHING) HOLTTUM, known from Assam, Tonkin and Thailand, but this cannot be regarded as certain, and I prefer to regard WILLDENOW's name as of doubtful application.

PRESL gave the name *Nephrodium sorbifolium* to two bathyphylls, representing two distinct species, collected by HAENKE in Luzon; I identify the specimens as *L. copelandii* and *L. pteroides*.

Excluded

Lomagramma praestantissimum (BORY) GRIES. Fl. Brit. W. Ind. (1864) 678 = *Neurocallis praestantissimum* (BORY) FÉE.

Lomagramma wilkesiana (BRACK.) COPEL. Philip. J. Sc. 3 (1908) Bot. 32 = *Teratophyllum wilkesianum* (BRACK.) HOLTTUM.

5. ELAPHOGLOSSUM

J.SM. in Hook. J. Bot. 4 (1841) 148, *nom. cons.*; in Hook. Gen. Fil. (1842) t. 105A; MOORE, Ind. Fil. (1857) xvi; *ibid.* (1862) 351; J.SM. Hist. Fil. (1875) 125; BEDD. Handb. Ferns Br. India (1883) 416; CHRIST, Farnkr. Erde (1897) 33; Neue Denkschr. Allg. Schweiz. Ges. Naturw. 36 (1899) 1–159; DIELS in E. & P. Nat. Pfl. Fam. 1, 4 (1899) 331; C.CHR. Ind. Fil. (1905) lii, 302; COPEL. Gen. Fil. (1947) 119; MORTON, Amer. Fern J. 45 (1955) 11; W. R. ANDERSON, Regn. Veget. 40 (1965) 18; HOLTTUM, Blumea 14 (1966) 317–326. — *Olfersia* PRESL, Tent. Pterid. (1836) 232, *p.p. max.*, *non* RADDI. — *Aconiopteris* PRESL, Tent. Pterid. (1836) 236. — *Acrostichum* (*non* L.) FÉE, Hist. Acrost. (1845) 8, 27. — *Dictyoglossum* J.SM. Bot. Mag. 72 (1846) Comp. 18. — *Acrostichum sect. Elaphoglossum* HOOK. Spec. Fil. 5 (1864) 195–241; HOOK. & BAKER, Syn. Fil. (1868) 400. — **Fig. 15–24.**

Rhizome creeping, in Malesian *spp.* usually dorsiventral and bearing 2-ranked fronds with a branch-bud at the base of each (some tropical American *spp.* with fronds in more than 2 ranks and a few with radially organized rhizome); young parts protected by *scales* which are usually cordate (often strongly) at the base, with edges bearing short teeth by projection of the wall between 2 adjacent cells, or hairs which may be of one or several cells, some cells usually glandular; outgrowth from the rhizome (in all Malesian *spp.*) forming similarly scaly terete *phyllopodia* to

which fronds are ± distinctly jointed (when dry, phyllopodia are usually darker than stipes). *Fronds* simple, entire, dimorphous, stipitate or sessile, usually ± coriaceous, often with a colourless cartilaginous thinner edge, costa usually somewhat prominent and grooved on upper surface, rounded and ± prominent on lower; veins conspicuous or not, forked once or twice, all branches almost reaching the margin, their tips in most *spp.* free and thickened, in a few *spp.* the vein-tips joining each other in a series of arcs just within the margin; small scales ± abundant, persistent or not, on both surfaces, in a few species peltate. *Fertile fronds* with smaller lamina than sterile, sometimes of different and distinctive shape, often with longer stipes than sterile, the lower surface quite covered with sporangia except for the thin decoloured margin and (in some species) a narrow decurrent part of the base. *Spores* with well-developed folded perispore.

Type species: *Acrostichum conforme* SW.

Distribution. More than 400 *spp.*, throughout wetter parts of tropics and subtropics, with greatest diversity on the Andes.

Ecology. Almost all Malesian species are epiphytes, though some will grow on mossy rocks in low forest at high altitudes; one is reported growing on wet rocks in a stream-bed (*E. resiniferum*); few if any grow in full exposure to the sun. They usually grow in association with other ferns and orchids on heavily-laden tree-branches; when seen at a distance their simple entire fronds often resemble orchid leaves and so may be overlooked. Few species occur in lowland forest, most at 1000–2500 m. The fronds of most are somewhat fleshy, with thick cuticle, and some are very rigid when dried; those with thinnest fronds occur in sheltered places, some on tree-trunks not far above ground level (*E. melanostictum*). The surface often shows a bluish hue. Fronds are shed when old by breaking at the joint between phyllopodium and stipe, where there is an internal change of structure though no true abscis-layer (see BELL, *infra*, 1951) and I believe that most fronds probably persist for more than a year, some possibly 2 years or more (old ones may bear a considerable growth of epiphyllous bryophytes). Fertile fronds are produced periodically, probably in response to dry weather, as in other genera of this group. I had a plant of *E. amblyphyllum* in cultivation in a hanging pot in Singapore for more than 20 years and only once saw a fertile frond on it, perhaps because it was always watered on rainless days (the species was native locally on old trees in mangrove but such trees are fast disappearing. R. M. LLOYD has discussed some aspects of the ecology of tropical American species (Amer. Fern J. 60, 1970, 73–82); at high altitudes only about 50% are epiphytic. Some species lack a joint at the base of a stipe; these were mostly epiphytic, not terrestrial.

Vegetative morphology and anatomy. P. R. BELL has published "Studies in the genus *Elaphoglossum*" in five papers, based largely on his own observations of tropical American species (Ann. Bot. n.s. 14, 1950, 545–555; *ibid.* 15, 1951, 333–346, 347–357; *ibid.* 19, 1955, 173–199; *ibid.* 20, 1956, 69–88). He dealt with stelar structure in relation to habit, vascular supply to roots and branches in relation to bases of fronds, the anatomy of fronds and structure of scales and hairs. He proceeded to arrange in series observations on 87 *spp.* relating to (a) stelar structure (dorsiventral with fronds in 2 or more ranks, or radially symmetrical), (b) development of the joint, and aerenchyma of the phyllopodium, (c) scales on the frond; and works out the frequencies of various combinations of characters, thereby indicating that the species of Malaya (which alone of Malesian *spp.* he compared with American *spp.*) show predominant a condition he regards as primitive, having a combination of dorsiventral rhizome with 2 ranks of fronds, phyllopodium with joint at its tip and aerenchyma near its base, and flat scales with basal attachment. So far as I have been able to observe, the other Malesian species agree in the 2-ranked arrangement of the fronds, which resemble that of young plants in the other genera of the group. I have not examined the aerenchyma of phyllopodia; the external characters associated with this are difficult to see clearly on dried specimens (and to examine them one needs to remove all scales) and should be studied by someone having access to abundant living plants.

Scales are important diagnostically, both on rhizome and surface of fronds; size, shape and colour are distinctive, also the nature of marginal hairs and the position of glandular cells. It appears that glandular cells of many species can produce a resinous exudation which may persist after the scale has fallen or become disintegrated. This also needs examination on living plants. A further comment on scales is given in the section on Taxonomy below.

Venation is often not easy to distinguish, especially the form of the ends of the veins which can usually only be seen if the frond is cleared with chloral hydrate. In a few species the ends of the veins anastomose just within the margin but these do not constitute a natural group and PRESL's genus *Aconiopteris*, based on this character, cannot be maintained; probably not all cases of this kind have yet been recognized, because of opacity of fronds.

Gametophyte. A. G. STOKEY and L. R. ATKINSON have published a study of gametophytes of 19 tropical American *spp.* (Phytomorphology 7, 1957, 275–292); these include one (*E. gayanum* (FÉE) MOORE) belonging to the group of *E. conforme*, which shows no peculiar characters (see *infra* on subdivision of

genus). Prothalli are slow-growing and long-lived, ribbon-like with crisped wings, marginal rhizoids and abundant short hairs with waxy caps; these wax-bearing hairs may be compared with glandular hairs on scales of the sporophytes. Marginal rhizoids are reported by STOKEY and ATKINSON as occurring also in *Selliguea* BORY and in Grammitoid ferns; their presence is perhaps an adaptation to epiphytic growth among mosses, and cannot be an indication of any close relationship between such very diverse genera as *Elaphoglossum*, *Selliguea* and *Grammitis*. Archegonia and antheridia "conform in type to those of the higher ferns". Gametophytes of *Elaphoglossum* are thus distinct from those of all other genera in the present group. It may be relevant that NAYAR found narrow ribbon-like gametophytes in *Microsorium pteropus* (BL.) CHING (*Polypodiaceae*) whereas the type species *M. punctatum* (L.) COPEL. has normal cordate ones. NAYAR separated *M. pteropus* as type of a distinct genus *Kaulinia*, but there is no reason to think that the two genera are not closely related (Taxon 13, 1964, 67–69).

Taxonomy. The generic name *Elaphoglossum* was proposed by SCHOTT in 1834 for certain specified species of the composite genus *Acrostichum*, but he gave no description, and therefore his name, though long accepted, does not comply with the present conditions of valid publication (MORTON, *l.c.* 1955). When PRESL attempted a more complete survey of the Acrostichoid ferns (1836) he adopted the name *Olfersia* RADDI for the species listed as *Elaphoglossum* by SCHOTT; but RADDI's name was given originally to the single species *O. corcovadensis*, which is now included in the earlier *Polybotrya* H. & B. PRESL also established a new genus *Aconiopteris* for *Acrostichum subdiaphanum* HOOK. & GREV., the only distinctive character of which is that the veins join in a series of arcs along the margin. This character is not now regarded as significant for generic separation, and the type species of *Aconiopteris* is now included in the same genus as most of those listed as *Olfersia* by PRESL. Thus, according to a strict interpretation of the Code, *Aconiopteris* is the correct name for the species which have been commonly called *Elaphoglossum* for more than a century. The first valid publication of the name *Elaphoglossum* was by JOHN SMITH in 1841. A proposal was therefore made (ANDERSON 1965) for the conservation of *Elaphoglossum* J.SM. as against *Aconiopteris* and this has been approved.

In 1845 FÉE published his elaborate and finely illustrated work on the Acrostichoid ferns, in which he criticized PRESL's arrangement. He restricted the genus *Olfersia* PRESL to two species and redefined *Acrostichum* to include the bulk of PRESL's *Olfersia*; for *Acrostichum* as restricted by PRESL (but excluding a few species) he proposed the new name *Chrysodium*. He maintained *Aconiopteris* as a separate genus. In 1846 JOHN SMITH published the name *Dictyoglossum* for tropical American species having anastomosing veins, but a generic separation on this character is now regarded as unnatural. In 1857 MOORE adopted the name *Elaphoglossum* in the modern sense and transferred many names to it, but HOOKER (1864) reverted to a comprehensive *Acrostichum* with *Elaphoglossum* as a section. BEDDOME (1865 onwards) followed MOORE, and the name *Elaphoglossum* came into quite general use after the publications of CHRIST (1897, 1899) and DIELS (1899).

Subsequent treatment of the genus in relation to other genera in systems of classification is dealt with in the introduction to the present group of genera (*supra* p. 257). One aberrant suggestion should however be mentioned. In his Monograph (1899, p. 17) CHRIST recognized the isolation of *Elaphoglossum* among Acrostichoid ferns, but pointed out similarities between the genera *Elaphoglossum* and *Syngramma*, noting however the great difference between the bristle-like hairs which clothe the rhizome of *Syngramma* and the scales of *Elaphoglossum*. BOWER accepted a relationship between the two genera, and placed them as simple-fronded derivatives of the same stock as *Metaxya* (The Ferns 1, 1928, 233–238). But the superficial resemblance between *Elaphoglossum* and *Syngramma* is due to the kind of convergent evolution that has occurred many times among ferns. It is clear that one general evolutionary trend which has occurred along several separate lines is reduction from a branched frond to a simple one; *Syngramma* and *Elaphoglossum* appear to be the ends of two quite different such lines. They differ greatly in spores as well as in scales; probably a study of sporangia would show further differences. The association of *Syngramma* (an exclusively Old World genus) and *Elaphoglossum* with *Metaxya*, which is an isolated monotypic south American genus placed with some doubt in a separate subfamily of *Cyatheaceae* (Fl. Males. II, 1, 1963, 72) seems to me highly improbable. I know of no other author who has seriously upheld BOWER's ideas on these genera.

Subdivision of the genus. PRESL (1836: 233–235) divided the species of his genus *Olfersia* into two 'phalanges': *frons herbacea* and *frons coriacea*. This is not a practicable arrangement. FÉE (1845) divided the species of his *Acrostichum* into two groups, *Oligolepideae* and *Polylepideae*. Though this also is not satisfactory, it seems to me to be in the right direction, namely to use the scales on the fronds as a basis for subdivision. The type species of the genus, *E. conforme*, comes into FÉE's *Oligolepideae*. If now we use characters of the scales, and not their abundance, to distinguish *E. conforme* and its allies from the species of FÉE's *Polylepideae*, we can have a clear-cut division; as almost all species of a re-defined *Polylepideae* have in fact conspicuously scaly fronds, the name is not inappropriate. It appears to me that this second division may be again subdivided on scale characters, as indicated below.

CHRIST (1899) divided the genus into two 'ordines', *Stenoneura* and *Condyloneura*, each ordo being divided into sections and subsections. The species of *Stenoneura* were said to have veins running to the margin without thickened tips, whereas in *Condyloneura* the veins are described as having thickened tips. In fact most species placed by CHRIST in *Stenoneura* are seen to have thickened vein-tips if the fronds are cleared with chloral hydrate, so that his main division is unreal; the minor subdivisions also are not more useful.

The following conspectus is tentative, for which reason I have not formally proposed any new names for subdivisions of the genus. The conspectus differs from that published by me in 1966 (Blumea 14: 319) owing to comments received from W. R. ANDERSON, University of Michigan, to whom I express my

thanks; he has made a far more thorough study of tropical American species than I could attempt. No doubt the present conspectus is over-simplified, and is not adequate to cover all tropical American species; it is intended only as a step towards more light on a complex problem.

1. Scales on frond bearing some marginal cells which are swollen and glandular, usually also bearing marginal hairs which consist of several cells, the terminal cell being glandular group of *E. conforme* (Sw.) J.Sm.
1. Scales on frond not bearing swollen glandular marginal cells except sometimes near the base; marginal hairs, if present, each consisting of a single cell which is usually acicular and thin-walled.
2. Scales on frond flat, with marginal hairs . . . . . group of *E. muscosum* (Sw.) Moore
2. Scales on frond narrow, with reflexed edges (at least in basal part), thus bristle-like, lacking marginal hairs . . . . . group of *E. spathulatum* (Bory) Moore

Malesian species. The earliest attempt at a comparative account of Malesian species was by Blume, who published full descriptions and excellent plates of those he knew in Java (Fl. Jav. Fil. 1829). But Blume adopted some earlier names, originally given to plants from other parts of the world which are distinct from the Java species (*e.g. Acrostichum decurrens*, *A. gorgoneum*, *A. viscosum*). Some other early names, notably *E. conforme* (described originally from St Helena) have also been used in too broad a sense. The result has been considerable confusion in the use of such names by past authors, and without reference to specimens one cannot always be sure of the sense in which such names have been used.

A few Malesian species are common in mountain forests, and have been frequently collected, especially *E. callifolium*, *E. angulatum* and *E. blumeanum*. Most other species have been collected too little for a really good assessment of their full range of variation, and of their geographical distribution. This is especially the case in New Guinea, where (in Malesia) the genus has its greatest diversity, and several species are known only from single collections, so that their descriptions may need subsequent modification. Further collections of good sterile specimens would help considerably. It appears that the most widely distributed Malesian species are *E. angulatum* (mountains of E. tropical Africa, Mascarene Is., Ceylon and S. India, throughout Malesia) and *E. callifolium* (throughout Malesia and eastwards to Fiji).

Almost all Malesian species belong to the group of *E. conforme* in the conspectus. A few belong to the group of *E. muscosum*, none to that of *E. spathulatum*, the nearest members of which are in Polynesia (*E. samoense* Brack., *E. rapaense* Copel., *E. societarum* Copel.) and in Africa (about 6 *spp.*), a curious distribution.

Key to Malesian species. Apart from separation of the few representatives of the group of *E. muscosum* (*nos* 45–48) the key which follows is not an attempt at a natural arrangement, but only an attempt to provide a means of identification, and is usable only for mature plants. Young plants often have fronds different in shape from older ones; in general, fronds on young plants have a lamina more gradually decurrent at the base and a broader apex than those on mature plants, and plants of immature size rarely have fertile fronds. The key should serve to identify most mature plants, whether or not they have fertile fronds. Fertile fronds are almost always narrower than sterile; in each species widths of the two are in a fairly constant ratio. A distinctive feature of fertile fronds in some species is that their stipes are much longer than those of sterile fronds, but this is not always a constant character. However, I believe that in general there is a good contrast between species in which the stipes of the two kinds of fronds are of similar length, and those in which the fertile stipes are twice (or more times) as long as the sterile ones.

Shape of fronds is always important, particularly the shape of the apex; there seems to be more variation in the base in some species. Size is also significant, but one must remember that plants of the same species in situations differing in altitude or in exposure may differ considerably in size, also in texture. Texture, and the degree of distinctness of veins, can be significant, especially extreme conditions, but many species are in an intermediate state between very thick and rather thin. The development of the colourless margin is certainly significant, though I think that a narrow margin of thick-walled colourless cells is always present. An anatomical study to show the relationship between internal structure and external form would be of interest, but is beyond the scope of the present work (an indication of the kind of anatomical structure which can occur at the margin of a frond is given by Bell, Kew Bull. 14, 1960, 81).

KEY TO THE SPECIES

1. Small scales on frond stellate or elongate, their marginal hairs glandular or with a glandular apical cell, thick-walled unicellular marginal hairs lacking; rhizome-scales various.
2. Lamina of sterile fronds rarely over 7 cm long; rhizome 1–2 mm ∅, fronds usually well-spaced on it.
3. Rhizome-scales light brown.
4. Sterile lamina elliptic, commonly 4–7 cm long, base decurrent as a narrow wing.
5. Fertile lamina spathulate, abruptly contracted at base and then decurrent as a narrow wing 2 cm long; rhizome-scales to 1 mm wide . . . . . **1. E. bolanicum**
5. Fertile lamina narrowly elliptic, little decurrent; rhizome-scales 2 mm wide **2. E. habbemense**
4. Sterile lamina ovate, almost same shape and size as fertile, *c.* 2 cm long . . . . **3. E. pumilum**
3. Rhizome-scales dark . . . . . **4. E. hellwigianum**
2. Lamina of sterile fronds usually more than 7 cm long; rhizome thicker.
6. Rhizome long-creeping with well-spaced fronds.
7. Apex of sterile fronds acute or short-acuminate.
8. Scales dark, glossy, 1 mm wide . . . . . **5. E. brunneum**
8. Scales thin, medium brown, 2–3 mm wide . . . . . **6. E. angulatum**

7. Apex of sterile frond rounded.
9. Rhizome-scales light brown; scales on frond red-brown . . . . . **7. E. pullenii**
9. Rhizome-scales dark brown; scales on frond dark, glossy (not known in *no* 9).
10. Rhizome-scales to 5 by $1^1/_2$ mm; stipe of sterile fronds 4–15 cm long . . **8. E. sclerophyllum**
10. Rhizome-scales shorter, less than 1 mm wide; stipe of sterile fronds 3–5 cm . . **9. E. repens**
6. Rhizome short, with closely-placed fronds.
11. Lamina of sterile frond decurrent to joint with phyllopodium or within 2 cm of joint.
12. Edge of sterile lamina conspicuously pale and thin, $^1/_2$ mm or more wide.
13. Sterile lamina twice as wide as fertile.
14. Apex of sterile frond bluntly pointed or rounded, base cuneate and then decurrent for 4–7 cm as a wing 1–2 mm wide on each side of costa . . . . . **10. E. ophioglossoides**
14. Apex of sterile frond short-acuminate, base narrowed evenly almost to joint with phyllopodium . . . . . **11. E. latemarginatum**
13. Sterile lamina little wider than fertile . . . . . **12. E. pellucido-marginatum**
12. Edge of sterile lamina not conspicuously pale and thin.
15. Sterile frond acuminate or apiculate.
16. Rhizome-scales 10–15 by 3–4 mm, light brown, thin; lamina widest above middle **13. E. thamnopteris**
16. Rhizome-scales much smaller, dark; lamina widest at middle.
17. Sterile frond *c.* 22 by 2 cm . . . . . **14. E. idenburgensis**
17. Sterile frond much larger, to $4^1/_2$ cm wide.
18. Apex of sterile frond acuminate.
19. Sterile frond 35–50 by $3^1/_2$–5 cm . . . . . **15. E. archboldii**
19. Sterile frond to 35 by 2.3 cm . . . . . **27. E. angustifrons**
18. Apex of sterile frond broad with a narrow apiculus 5 mm long . . . **16. E. apiculatum**
15. Sterile frond not acuminate nor apiculate.
20. Sterile frond widest $^1/_3$ from apex, narrowed rather abruptly to broad-pointed apex.
21. Rhizome-scales 15–20 mm long, 2 mm wide; fronds thick, veins obscure; costa broad and little prominent on lower surface. . . . . **17. E. annamense**
21. Rhizome-scales not over 10 mm long; fronds rather thin, veins distinct; costa slender and prominent on lower surface.
22. Scales on surface of frond pale, bearing slender hairs 1 mm long; stipe of fertile frond 10–15 cm . . . . . **18. E. melanostictum**
22. Scales on frond dark, bearing very short hairs; stipe of fertile frond 25–30 cm **19. E. heterostipes**
20. Sterile frond widest about middle, or if above middle narrowed gradually to a rounded apex.
23. Sterile frond widest at middle, apex acute; fertile frond to 2 cm wide **20. E. calanasanicum**
23. Sterile frond widest a little above middle, gradually narrowed to rounded apex; fertile fronds not over 1.3 cm wide . . . . . **21. E. norrisii**
11. Lamina of sterile frond not thus decurrent.
24. Scales on rhizome dark, rigid, glossy.
25. Small scales on upper surface of frond dark, glossy, elongate, with dark rigid cylindrical marginal hairs each consisting of one cell with a small thin-walled cell at its apex.
26. Scales on lamina 1–2 mm long; fronds with broadly rounded apex . . . . **22. E. apoense**
26. Scales on lamina much smaller; apex of fronds not broadly rounded . . **23. E. vepriferum**
25. Small scales on upper surface otherwise, at least some of their marginal hairs multicellular with glandular apical cell.
27. Apex of sterile frond rounded.
28. Phyllopodia $^1/_2$–1 cm long; lamina of sterile frond always *c.* 10 times as long as wide.
29. Scales on costa and stipe appressed, on lamina very small . . . . . **24. E. nigripes**
29. Scales on stipe and costa spreading, on lamina 1–2 mm long, abundant **25. E. melanochlamys**
28. Phyllopodia $1^1/_2$–2 cm long; lamina of sterile frond often proportionately broader **8. E. sclerophyllum**
27. Apex of sterile fronds acute or acuminate.
30. Lamina of sterile frond *c.* 10 times as long as wide.
31. Rhizome-scales less than 1 mm wide, somewhat crisped; stipe of fertile frond not or little longer than that of sterile . . . . . **26. E. nesioticum**
31. Rhizome-scales more than 1 mm wide, flat; stipe of fertile frond usually twice as long as sterile.
32. Sterile frond $3^1/_2$–5 cm wide, 35–50 cm long . . . . . **15. E. archboldii**
32. Sterile frond to 2.3 cm wide, 35 cm long . . . . . **27. E. angustifrons**
30. Lamina of sterile frond *c.* 5 times as long as wide.
33. Rhizome bearing fronds 5–10 mm apart; scales 6 by 1 mm; sterile lamina widest below middle, rather abruptly contracted at base, apex short-pointed . . . . **5. E. brunneum**
33. Rhizome bearing fronds close together; scales 10 by $1^1/_2$ mm; sterile lamina widest at middle, base rather narrowly cuneate, apex acuminate . . . . . **28. E. pallescens**
24. Scales on rhizome medium to light brown, mostly rather thin.

34. Lower surface of sterile lamina covered with a felt of narrow scales 2–3 mm long **29. E. arachnoideum**
34. Lower surface of lamina bearing smaller, usually appressed, scales.
35. Fronds of adult plants widest above middle, with rounded apices and decurrent bases.
36. Fronds lacking a fringe of spreading scales.
37. Rhizome-scales less than 1 mm wide . . . . . **30. E. stenolepis**
37. Rhizome-scales 2 mm or more wide . . . . . **31. E. amblyphyllum**
36. Fronds bearing a fringe of spreading scales . . . . . **32. E. luzonicum**
35. Fronds of adult plants, if widest above middle, rather much narrowed upwards, apex not broadly rounded.
38. Sterile fronds with distinct thin pale edge which bears abundant scales 1–1 1/2 mm long, persistent on young plants, mostly lost on old ones . . . . . **32. E. luzonicum**
38. Sterile fronds without a fringe of scales.
39. Sterile lamina twice as long as wide (to 12 by 6 cm); stipe of fertile frond as long as sterile frond with its stipe . . . . . **33. E. brevifolium**
39. Not this combination of characters.
40. Apex of sterile frond distinctly pointed, point broad or acute.
41. Sterile frond widest in distal half, base very gradually and evenly narrowed, stipe to 5 cm long . . . . . **19. E. heterostipes**
41. Sterile frond widest at or below middle, base otherwise, stipe in most cases longer.
42. Pale margin of sterile frond thin, flat, 1/2 mm wide or nearly so.
43. Fronds widest below middle, narrowed gradually to apex; veins distinct **34. E. negrosensis**
43. Fronds widest at middle, apex obtuse-angled; veins not distinct **35. E. planicosta**
42. Pale margin of sterile frond very narrow, usually reflexed.
44. Scales to 1 1/2 mm wide, not flat.
45. Scales straight and rather stiff with inrolled edges; frond commonly 35 cm or more long, narrowly elliptic . . . . . **36. E. callifolium**
45. Scales thin, crisped throughout, with long twisted hair-points; frond rarely 30 cm long, broadly elliptic . . . . . **37. E. commutatum**
44. Scales wider, flat or little crisped, edges not inrolled.
46. Stipe of fertile frond not much longer than stipe of sterile.
47. Scales commonly 20–25 by 2 1/2–3 mm . . . . . **38. E. malayense**
47. Scales not over 10 mm long.
48. Rhizome-scales with many spreading marginal hairs; scales on lamina to 1 mm long, narrow . . . . . **40. E. sordidum**
48. Rhizome-scales with few marginal hairs; scales on lamina stellate, under 1/2 mm long.
49. Costa broad and not prominent beneath; rhizome-scales firm **41. E. novoguineense**
49. Costa prominent beneath; rhizome-scales thin, with isodiametric cells **43. E. favigerum**
46. Stipe of fertile frond at least twice as long as stipe of sterile.
50. Scales 6 by 2 1/2 mm, sterile frond short-acuminate . . . . **39. E. recommutatum**
50. Scales to 15 by 2 mm; sterile frond broadly pointed . . . . . **42. E. robinsonii**
40. Apex of sterile frond distinctly rounded.
51. Rhizome-scales 3–5 mm long; fertile frond *c.* 8 by 3.3 cm . . . . . **7. E. pullenii**
51. Rhizome-scales 10–15 mm long; fertile frond at least 6 times as long as wide.
52. Spores 52–59 μm long with broad perispore of few folds; stipe of fertile frond twice as long as that of sterile; edge of lamina thick, deflexed; lamina greenish when dry.
53. Lamina of sterile frond to 30 by 5 cm, stipe 5–8 cm long. . . . **44. E. sumatranum**
53. Lamina of sterile frond 35–55 cm long, stipe 14–18 cm long . **45. E. indrapurae**
52. Spores *c.* 37 μm long with narrow much-folded perispore; stipe of fertile fronds not much longer than of sterile; pale edge of lamina thin; fronds brownish when dry, thick, rigid **46. E. spongophyllum**

1. Small scales on frond (except near edge) ± orbicular, pale, with marginal teeth or hairs each of one thick-walled cell, not glandular; rhizome-scales always narrow, rigid, dark, glossy.
53. Scales on upper surface conspicuously stellate; sterile fronds often to 3 cm wide.
54. Scales on lower surface very small, each with 3–5 marginal hairs 1/2–1 mm long spreading away from frond-surface . . . . . **47. E. blumeanum**
54. Scales on lower surface with a distinct lamina (flat or not) bearing more slender and shorter marginal hairs.
55. Scales of lower surface mostly elongate, bullate at base; on upper surface flat, those near margin elongate, forming a conspicuous spreading fringe . . . . . **48. E. miniatum**
55. Scales of lower surface small, orbicular, flat or cup-shaped; scales of upper surface flat, about same size as on lower, those near margin not forming a conspicuous fringe **49. E. heterolepium**
53. Scales on upper surface with very short marginal hairs; sterile fronds *c.* 1 cm wide **50. E. resiniferum**

1. Elaphoglossum bolanicum ROSENST. in Fedde, Rep. 12 (1913) 180; v.A.v.R. Handb. Suppl. (1917) 427; COPEL. Philip. J. Sc. 78 (1949) 403. — Type: KEYSSER B.62, Bolan Mts, NE. New Guinea (S-PA). — **Fig. 15.**

Rhizome long-creeping, 1–1$^1/_2$ mm ∅; fronds 1–2 cm apart; scales thin, light brown, to 3 by 1 mm, edges with few short hairs; phyllopodia 6–8 mm long. *Sterile frond:* stipe 2–3$^1/_2$ cm; lamina 4–7 cm by 9–13 mm, widest at or below middle, gradually narrowed distally, apex acute, towards base similarly narrowed and then decurrent as a narrow wing for 10–15 mm; pale thin edge distinct; veins visible but not prominent; scales on both surfaces minute, dark brown, with short spreading hairs. *Fertile frond:* stipe 4–6 cm; lamina 2$^1/_2$–3 cm by 9–12 mm, widest $^1/_3$ from base, narrowed to blunt apex and more abruptly to base, with narrow basal wing as sterile.

Distr. *Malesia:* NE. New Guinea (3 collections).

Ecol. At 2400–3000 m.

Note. The type specimen has only one sterile frond, which is smaller than the fertile ones; sterile fronds are described above from the other collections, which agree exactly in rhizome-scales and in fertile fronds with the type.

Fig. 15. *Elaphoglossum bolanicum* ROSENST. *a.* Habit, 2 sterile fronds, 1 fertile, × $^2/_3$, *b.* scale from rhizome, × 13, *c.* scale from surface of frond, × 27 (HOOGLAND & SCHODDE 7699).

2. Elaphoglossum habbemense COPEL. Univ. Cal. Publ. Bot. 18 (1942) 226; Philip. J. Sc. 78 (1949) 403, pl. 7. — Type: BRASS 9083, W. New Guinea, Lake Habbema (GH).

Rhizome long-creeping, *c.* 2 mm ∅, fronds 1–2 cm apart; scales light brown, translucent, closely imbricating, 3 by 2 mm, ovate, acute, subentire; phyllopodia to 8 mm long. *Sterile frond:* stipe 2–3 cm; lamina 3$^1/_2$–6 cm by 8–15 mm, thinly coriaceous to rigid, elliptic, apex bluntly pointed, base narrowly cuneate and then decurrent as a wing 10–15 mm; thin edge distinct, narrow; veins visible or not; costa slightly prominent beneath; scales on costa beneath rather persistent, narrowly acuminate from a broad base, $^1/_2$–1$^1/_2$ mm long; scales on lower surface of lamina stellate, smaller. *Fertile frond:* stipe 1$^1/_2$–3$^1/_2$ cm; lamina 2$^1/_2$–4$^1/_2$ cm by 7–10 mm, shape as sterile.

Distr. *Malesia:* New Guinea (3 collections).

Ecol. In a cushion of hepatics on exposed tree-branch, 3225 m.

3. Elaphoglossum pumilum LAM & VERHEY, Blumea 5 (1945) 559, f. 2. — Type: MONOD DE FROIDEVILLE 253, Lompobatang, Bonthain, S. Celebes (L; dupl. in BO).

Rhizome slender, creeping, bearing fronds $^1/_2$–1 cm apart; scales brown, thin, entire, ovate-acute, to 2$^1/_2$ mm long; phyllopodia 5 mm long. *Sterile frond:* stipe 2 cm; lamina to 2 by 1 cm, thinly coriaceous, ovate, base shortly decurrent as a narrow wing, apex blunt, rounded; thin pale edge narrow, ± reflexed; veins slightly prominent beneath; costa hardly prominent on lower surface; no superficial scales seen. *Fertile frond:* stipe 3$^1/_2$–6 cm; lamina to 20 by 9 mm, shape as sterile.

Distr. *Malesia:* S. Celebes. Only known from type collection.

Ecol. At 2500 m.

4. Elaphoglossum hellwigianum ROSENST. Nova Guinea 8 (1912) 731; v.A.v.R. Handb. Suppl. (1917) 423; COPEL. Philip. J. Sc. 78 (1949) 403. — Type: VON RÖMER 1273, Hellwig Mts, W. New Guinea (S-PA; dupl. in BO).

Rhizome 2 mm ∅, fronds *c.* 1 cm apart; scales rigid, dark, glossy, narrow, acuminate, 2–3 mm long, edges with short teeth or sparse short hairs; phyllopodia not distinct. *Sterile frond:* stipe 1–1$^1/_2$ cm; lamina rigid-coriaceous, 3 by 1$^1/_2$ cm, almost elliptical, base slightly decurrent, apex broadly pointed (fronds on a young plant obovate with much-decurrent bases); thin pale edge distinct; veins not visible; costa slightly prominent near base beneath; many scales on lower surface of young frond (mostly caducous), dark, elongate, with some marginal hairs. *Fertile frond:* stipe 3 cm; lamina 1$^1/_2$ by 1 cm, elliptic, base hardly decurrent; small dark glossy scales abundant among sporangia.

Distr. *Malesia:* W. New Guinea. Only known from type collection.

Ecol. Probably at 3000 m or more.

5. Elaphoglossum brunneum COPEL. Univ. Cal. Publ. Bot. 18 (1942) 226; Philip. J. Sc. 78 (1949) 405, pl. 10. — Type: BRASS 12808, Idenburg River, W. New Guinea (GH).

Rhizome bearing fronds 5–10 mm apart; scales dark brown, glossy, rigid, 6 by 1 mm, narrowed to a hair-tip; phyllopodia 10 mm long. *Sterile frond:* stipe 8–10 cm; lamina rigid, to 19 by 4 cm, widest below middle, ± abruptly narrowed at base and

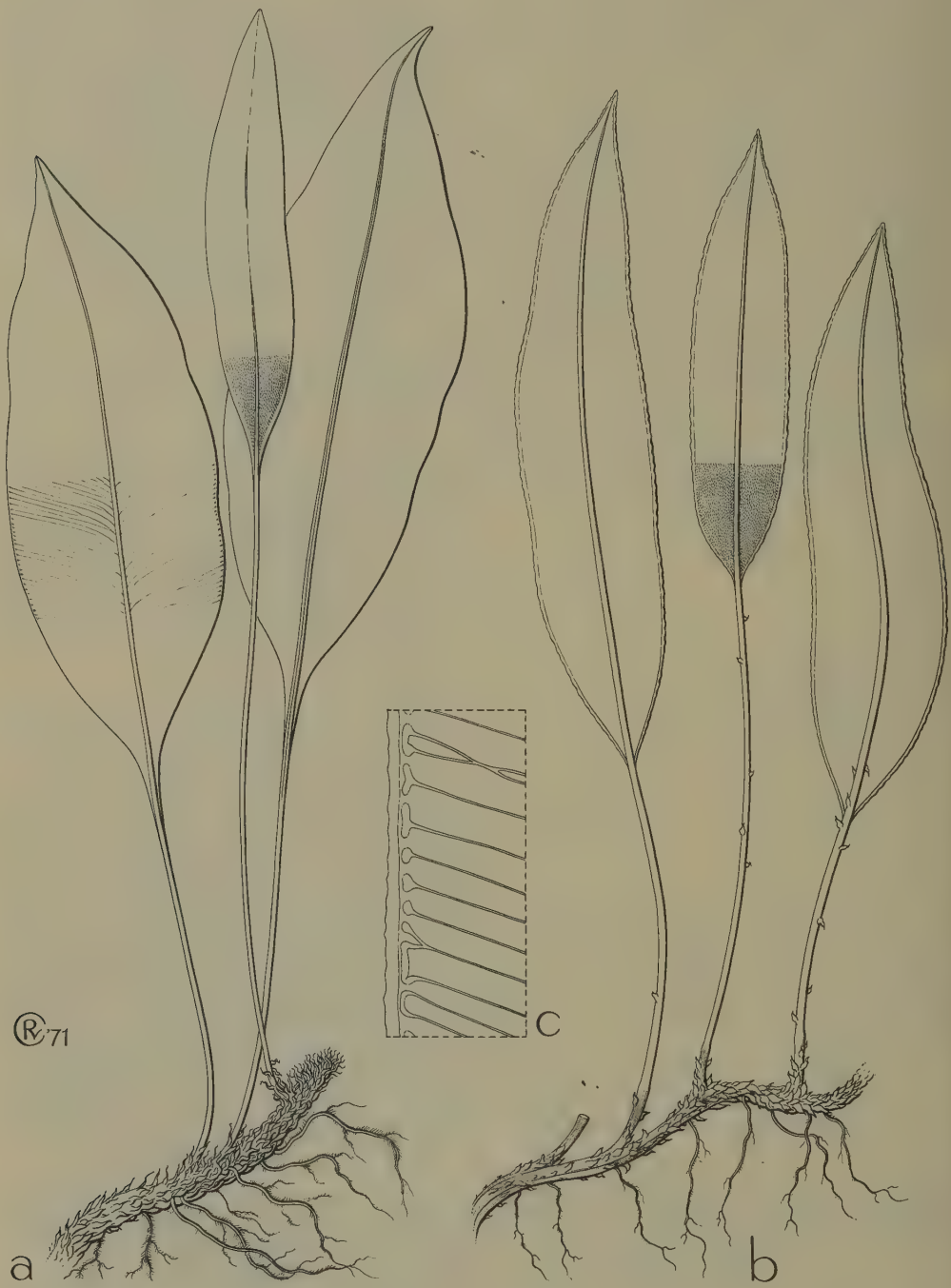

Fig. 16. *Elaphoglossum commutatum* (METT. *ex* KUHN) v.A.v.R. *a*. Habit, × 1/2. — *E. angulatum* (BL.) MOORE. *b*. Habit, × 1/2, *c*. margin of sterile frond, × 5 (*a* SURBECK 277, *b–c* L 908.331–949).

then slightly decurrent, more gradually to acute but not acuminate apex; pale edge *c.* 1/4 mm wide; veins just distinct; costa prominent and rounded beneath; scales on both surfaces appressed, dark, less than 1 mm long, elongate with a few short marginal hairs. *Fertile frond:* stipe 18 cm; lamina 12 by 2.2 cm, shape as sterile.

Distr. *Malesia:* W. New Guinea. Only known from type collection.

Ecol. Low epiphyte in rain-forest at 1200 m.

6. Elaphoglossum angulatum (Bl.) Moore, Ind. Fil. (1857) 5; v.A.v.R. Handb. (1908) 713; Suppl. (1917) 423; C.Chr. Gard. Bull. S. S. 7 (1934) 290; Backer & Posth; Varenfl. Java (1939) 250; Tard.-Bl. & C.Chr. Fl. Gén. I.-C. 7, 2 (1941) 541; Copel. Philip. J. Sc. 78 (1949) 405; Fern Fl. Philip. (1960) 278; Sledge, Bull. Brit. Mus. (Nat. Hist.) 4 (1967) 83. — *Acrostichum angulatum* Bl. En. Pl. Jav. (1828) 101; Fl. Jav. Fil. (1828) 25, t. 6; Fée, Hist. Acrost. (1845) 32; Racib. Fl. Btzg 1 (1898) 47. — *Olfersia angulata* Presl, Tent. Pterid. (1836) 234. — Type: Blume, Java (L).

E. minahassae v.A.v.R. Handb. Suppl. (1917) 527; Bull. Jard. Bot. Btzg II, 28 (1918) 24. — *Acrostichum conforme* (*non* Sw.) Christ, Ann. Jard. Bot. Btzg 15 (1898) 174, *p.p.* — Type: Koorders 17097, Menado, Celebes (BO).

E. dolichocaulon v.A.v.R. Bull. Jard. Bot. Btzg III, 5 (1922) 203; Backer & Posth. Varenfl. Java (1939) 250. — Type: Jeswiet 348, Mt Jang (BO).

E. ogatai C.Chr. Dansk Bot. Ark. 9, 3 (1937) 67. — Type: Ogata 59, Taiwan (BM).

E. alstonii Tard.-Bl. Not. Syst. Paris 15 (1959) 433. — *Acrostichum laurifolium* (*non* Thouars) Fée, Hist. Acrost. (1845) 36, t. 7, f. 1. — Type: Sieber, Mauritius (P).

E. laurifolium [*non* (Thouars) Moore] Bedd. Ferns S. India (1866) t. 200. — *E. latifolium* [*non* (Sw.) J.Sm.] Bedd. Handb. Ferns Br. India (1883) 416, *p.p.* incl. f. 248. — **Fig. 16b, c.**

Rhizome long-creeping, bearing fronds 1–3 cm apart; scales thin, light brown, 4 by 2–3 mm, triangular, tip blunt to acute, edges subentire; phyllopodia 1–2 cm long. *Sterile frond:* stipe 5–15 cm, when young scaly as rhizome; lamina thin but firm, 11 by 3 to 28 by 5 cm, narrowly elliptic (largest with sides parallel in middle part), apex short-acuminate, base slightly decurrent; thin edge nearly 1 mm wide, translucent; veins at a rather wide angle, distinct on lower surface, their ends joining a thickened submarginal band in which they bifurcate and form a ± continuous vascular commissure; costa not very prominent beneath; mature fronds glabrous except for a few scales on or near costa beneath, as those on stipe but smaller. *Fertile frond:* stipe to 18 cm or more long; lamina 13 by 2.2 to 22 by 3 1/2 cm, base more abruptly contracted than sterile, thin edge somewhat narrower.

Distr. E. tropical Africa, Madagascar, Réunion, Ceylon, S. India, Tonkin, Taiwan; throughout *Malesia* on higher mountains (not in the Malay Peninsula); New Hebrides.

Ecol. Epiphyte in low forest and sometimes on mossy rocks in ± sheltered places, at 2000–3500 m.

Note. The sterile frond of the Bogor type specimen of *E. minahassae* has a damaged apex which has a falsely rounded appearance; a Leiden specimen of the same number has fronds typical of *E. angulatum*. This is the most widely distributed Malesian species.

7. Elaphoglossum pullenii Holttum, Blumea 14 (1966) 324. — Type: Pullen 5034, *partim*, NE. New Guinea (L).

Rhizome creeping, fronds in each rank 1–1 1/2 cm apart; scales light brown, firm, ovate-acuminate, 5 by 1 1/2 mm, edges with few hairs; phyllopodia 1–1 1/2 cm long. *Sterile frond:* stipe slender, 13–14 cm long, glabrescent; lamina thick, rigid, to 12 by 3 cm, almost evenly elliptical, base shortly decurrent, apex narrowly rounded; thin pale edge *c.* 1/4 mm wide; veins ± distinct, not prominent; costa beneath broad, pale, hardly prominent; scales on lower surface red-brown, to 1 mm long, narrow with long marginal hairs near base, smaller ones stellate. *Fertile frond:* stipe 14 cm; lamina 6 by 2 to 8 by 3.3 cm, widest below middle, base abruptly narrowed and then decurrent 1 cm, apex broadly rounded.

Distr. *Malesia:* E. & NE. New Guinea.

Ecol. Epiphyte, low on trees in mossy forest at 3140–3300 m, growing with *E. angulatum*, a specimen of which was collected with the type.

8. Elaphoglossum sclerophyllum v.A.v.R. Nova Guinea 14 (1924) 22; Copel. Philip. J. Sc. 78 (1949) 405. — Type: Lam 1793, W. New Guinea (BO; dupl. in L, U).

E. fuscum Copel. Univ. Cal. Publ. Bot. 18 (1942) 226; Philip. J. Sc. 78 (1949) 406, pl. 12. — Type: Brass 9088, W. New Guinea (MICH; dupl. in BM, BO, GH, K, L).

E. laticuneatum Copel. Univ. Cal. Publ. Bot. 18 (1942) 226; Philip. J. Sc. 78 (1949) 405, pl. 9. — Type: Brass & Meijer-Drees 10032, W. New Guinea (GH).

Rhizome creeping, fronds 1–2 cm apart; scales rigid, dull brown to glossy dark brown, 4–6 by 1–1 1/2 mm, apex acuminate, edges with teeth or stiff hairs; phyllopodia 1 1/2–2 cm long. *Sterile fronds:* stipe 4–15 cm long, pale, rather persistently scaly as rhizome; lamina thick, rigid, variable in shape, commonly 10–13 by 2 1/2–3 1/2 cm, on some plants 8–10 by 4 cm, widest about middle or above it, apex narrowed to rounded tip, base cuneate and ± decurrent (more so in small than in large fronds); thin edge pale, 1/4 mm wide; veins distinct or not; costa broad and slightly prominent beneath; scales on both surfaces at first abundant, to 1 mm long, dark, glossy, appressed, usually with some spreading marginal hairs. *Fertile frond:* stipe 15–30 cm; lamina commonly 9–14 cm long, 2–2 1/2 cm wide, of one specimen 8 by 4 cm.

Distr. *Malesia:* New Guinea.

Ecol. On terrestrial moss-cushions or epiphytic in open thickets at *c.* 3000 m (several collections).

Note. A specimen at Leiden from W. New Guinea (Versteegh BW 12609, *partim*, Arfak Mts, 1750 m) has apparently a short thick rhizome with close fronds which are larger than those of the type (sterile to 18 by 4, fertile to 20 by 2 cm) but in shape and scaliness very similar. Brass collections from near Lake Habbema at 2000 m (11038, 13040) are similar. These may constitute a distinct species which occurs at about 2000 m.

9. Elaphoglossum repens COPEL. Univ. Cal. Publ. Bot. 18 (1942) 226; Philip. J. Sc. 78 (1949) 406, pl. 11. — Type: BRASS 12124, W. New Guinea, near Idenburg River (MICH; dupl. in GH, L).

Rhizome 2 mm ∅, creeping; fronds $^1/_2$–2 cm apart; scales dark brown, glossy, rigid, entire, to 3 by $^2/_3$ mm, narrowly acuminate; phyllopodia 1 cm long. *Sterile frond:* stipe slender, pale, 3–8 cm long; lamina thinly coriaceous, 12 by $2^1/_2$–3 cm, widest at middle, base ± decurrent, apex gradually narrowed to a ± broadly rounded tip; pale thin edge distinct; veins not prominent, sometimes distinct; costa slightly prominent beneath; surfaces glabrescent. *Fertile frond:* stipe 9–14 cm; lamina probably to 9 by $1^1/_2$ cm (larger frond broken), apex narrowly rounded, base a little decurrent.

Distr. *Malesia:* W. New Guinea. Only known from type collection.

Ecol. Frequent low epiphyte in mossy forest, 1800 m.

10. Elaphoglossum ophioglossoides (GOLDM.) HOLTTUM, Kalikasan, Philip. J. Biol. 3 (1974) 197. — *Acrostichum ophioglossoides* GOLDM. Nova Acta 19, Suppl. 1 (1843) 451. — Type: MEYEN *s.n.*, Manila (B).

E. merrillii CHRIST, Philip. J. Sc. 3 (1908) Bot. 275; v.A.v.R. Handb. Suppl. (1917) 424; COPEL. Fern Fl. Philip. (1960) 279. — Type: MERRILL 5853, Mt Halcon, Mindoro (P; dupl. in GH).

Rhizome short, fronds very close; scales medium brown, rather thin and crisped, hair-pointed, to 15 by 1 mm, edges with a few spreading hairs; phyllopodia less than 1 cm. *Sterile frond:* stipe 3–8 cm long with a wing *c.* 1 mm wide throughout, edge of wing pale cartilaginous as edge of lamina; lamina coriaceous, to 26 cm long, largest fronds $3^1/_2$–5 cm wide, usually widest above middle, narrowed gradually to base and more abruptly to broadly pointed or almost rounded apex; thin pale edge *c.* $^1/_2$ mm wide; costa beneath slightly prominent near base, distally flat; veins faintly visible; lower surface glabrescent, residual scales stellate, small. *Fertile frond:* stipe to 8 cm; lamina *c.* 10 by $1^1/_2$–2 cm.

Distr. *Malesia:* Philippines (Luzon, Mindoro, Samar).

Ecol. In forest, at 500 m, and probably higher.

Note. In 'Reise um der Erde' 2 (1855) 264–270, MEYEN described his ascent of Mt Sembrano above Laguna (480–510 m) from Manila; he appears not to have climbed higher mountains. The above description is taken mainly from the type collection of *E. merrillii* (P, GH); MEYEN's type is smaller but certainly represents the same species.

11. Elaphoglossum latemarginatum HOLTTUM, Blumea 14 (1966) 322. — Type: BRASS 24896, Papua, Goodenough I. (A).

Rhizome short; scales 8–10 by $1^1/_2$ mm, dull medium brown, rather thin, acuminate, apices sometimes a little twisted, edges with scattered hairs; phyllopodia 5 mm long. *Sterile frond:* wingless stipe pale, *c.* 1 cm long; lamina thinly coriaceous, 19–23 by 2.6–3.3 cm, widest $^1/_3$ from apex, narrowed very gradually to base which forms a gradually narrowing wing so that junction with stipe is indistinct, apex shortly acuminate; thin pale edge $^1/_2$ mm wide; veins distinct on lower surface; costa pale, not prominent on lower surface; scales on surface appressed, ± stellate with several short arms, mostly less than 1 mm ∅ including arms. *Fertile frond:* stipe 4 cm; lamina 17 by 1.6 cm, shape as sterile, thin pale margin 1 mm wide.

Distr. *Malesia:* E. New Guinea (Goodenough I.). Only known from type collection.

Ecol. Common low epiphyte on mossy trees, 1600 m.

12. Elaphoglossum pellucido-marginatum (CHRIST) C.CHR. Bot. Jahrb. 66 (1933) 65. — *Acrostichum pellucido-marginatum* CHRIST, Verh. Naturf. Ges. Basel 11 (1895) 255. — *Acrostichum gorgoneum* (*non* KAULF.) CHRIST, Ann. Jard. Bot. Btzg 15 (1898) 175, *p.p.*; v.A.v.R. Handb. (1908) 712, *p.p.* — Type: SARASIN 947, Celebes (BAS).

Rhizome-scales 5 by 1 mm, medium brown, ovate-acute; phyllopodia 5–10 mm long. *Sterile frond:* stipe (unwinged) to $2^1/_2$ cm; lamina of largest fronds 17 by $1^1/_2$ to 35 by 4 cm, firm but not thick, widest in upper third, gradually narrowed to decurrent base and more abruptly to narrowly rounded or broadly pointed apex; translucent edge *c.* $^3/_4$ mm wide; veins not very distinct, their free apices thickened; scales on lower surface very small, stellate. *Fertile frond:* stipe $3^1/_2$–10 cm; lamina almost as large as sterile, apex sometimes more distinctly rounded.

Distr. *Malesia:* North to SE. and SW. Celebes.

Ecol. Epiphyte, at 1200–2400 m.

Note. The species *E. gorgoneum* (KAULF.) BRACK. is confined to Hawaii (see p. 313).

13. Elaphoglossum thamnopteris HOLTTUM, Blumea 14 (1966) 326. — Type: BRASS 22990, Papua, Mt Dayman, 1650 m (A).

Rhizome short; scales 10–15 by 3–4 mm, rather thin, light brown, subentire, not acuminate; phyllopodia *c.* 1 cm long. *Sterile frond:* lamina rather thin, of specimens seen to 57 by $5^1/_2$ cm (to 80 cm long, *fide* BRASS), widest above middle, very gradually narrowed to joint with phyllopodium, apex acuminate; thinner edge hardly decoloured; veins distinct and slightly prominent on both surfaces, their apices joining in a series of submarginal arcs as in *Asplenium nidus*; costa prominent beneath throughout; scales on surfaces scattered, mostly under $^1/_2$ mm, with a few short marginal hairs and spherical cells near point of attachment. *Fertile frond:* stipe 15 cm; lamina 25 by 2 cm, base long-decurrent, apex shortly blunt-pointed.

Distr. *Malesia:* New Guinea, Ceram.

Ecol. Epiphyte (type in *Nothofagus* forest), at 1500–1700 m.

Note. A specimen from 2900 m in NE. New Guinea (T. G. WALKER 7571) has fronds to 35 by 4 cm, thicker than those of the type, but appears to belong to this species.

14. Elaphoglossum idenburgensis HOLTTUM, Blumea 14 (1966) 321. — Type: BRASS 12283, W. New Guinea (GH; dupl. in MICH).

Rhizome short; scales dark, glossy, rigid, to 4 by 2 mm; phyllopodia 12–17 mm long. *Sterile frond:* lamina rigid, decurrent to joint with phyllopodium, $21^1/_2$–1.8 cm, widest about middle,

base rather narrowly decurrent, apex acuminate; thin margin not decoloured, narrow, reflexed; veins rather obscure; costa prominent beneath; scales on both surfaces sparse, dark, appressed, usually entire. *Fertile frond:* stipe 6 cm; lamina 12 by 1.1 cm, base decurrent, apex bluntly pointed.

Distr. *Malesia:* W. New Guinea. Only known from type collection.

Ecol. In mossy forest on old log, 1800 m.

15. Elaphoglossum archboldii COPEL. Univ. Cal. Publ. Bot. 18 (1942) 226; Philip. J. Sc. 78 (1949) 404, pl. 8. — Type: BRASS 13220, W. New Guinea (GH).

Rhizome short; scales dark, glossy, rigid, flat, ovate, 4–5 by 1–1 1/2 mm; phyllopodia 2–4 cm long. *Sterile frond:* unwinged stipe 1–3 (to 8?) cm long, above which is a narrowly winged part 4–20 cm long below lamina; lamina thinly coriaceous, 25–50 by 2 1/2–5 cm, widest about middle, gradually narrowed to narrowly cuneate base, apex acuminate; thin edge not distinct; veins slightly prominent, their ends joining in submarginal arcs (at least near base of frond); costa prominent beneath; scales on lower surface not persistent, very small, stellate with arms of 2–3 cells. *Fertile frond:* stipe 10–30 cm long; lamina 20–30 cm long including a narrow sterile decurrent base, 2.2 cm wide.

Distr. *Malesia:* W. New Guinea.

Ecol. Epiphytic at 850–2000 m (type, at 850 m, a low epiphyte; specimen from 2000 m an epiphyte in moss cushions).

16. Elaphoglossum apiculatum HOLTTUM, Blumea 14 (1966) 320. — Type: BRASS 13624, W. New Guinea (GH).

Rhizome short; scales dark, glossy, rather broad (no complete ones seen); phyllopodia 1 1/2–2 cm long. *Sterile frond:* unwinged stipe less than 2 cm long; lamina (including basal wing) to 30 by 4.7 cm, thinly coriaceous, the main part (18 cm long) elliptic with a narrow triangular apiculus 5 mm long, at the base rather abruptly narrowed to the basal wing; thin edge not distinct; veins slightly prominent on both surfaces, sometimes anastomosing at their tips; costa strongly prominent beneath; scales on lower surface of lamina not seen, on lower surface of costa small, stellate, also a few larger appressed ovate dark glossy scales hardly 1 mm long. No complete *fertile frond* seen; one frond fertile in distal 8 cm, this fertile part contracted, 2.3 cm wide, basal part shaped as sterile but narrower.

Distr. *Malesia:* W. New Guinea. Only known from type collection.

Ecol. Epiphyte in rain-forest, at 900 m.

Note. This specimen is near *E. archboldii*, but differs in the shape of both apex and base of sterile fronds, characters which are usually distinctive in this genus.

17. Elaphoglossum annamense C.CHR. & TARD.-BL. Not. Syst. Paris 8 (1939) 209. — Type: POILANE 23783, S. Vietnam (P).

E. decurrens var. crassum C.CHR. Gard. Bull. S. S. 7 (1934) 290, *p.p.* — **Fig. 17.**

Rhizome short; scales dense, to 20 mm long, 2 mm wide at base, distally very narrow, hair-pointed, somewhat red-brown, older ones darker

Fig. 17. *Elaphoglossum annamense* C. CHR. & TARD.-BL. Three sterile fronds, one fertile, × 1/2 (KOSTERMANS 2412).

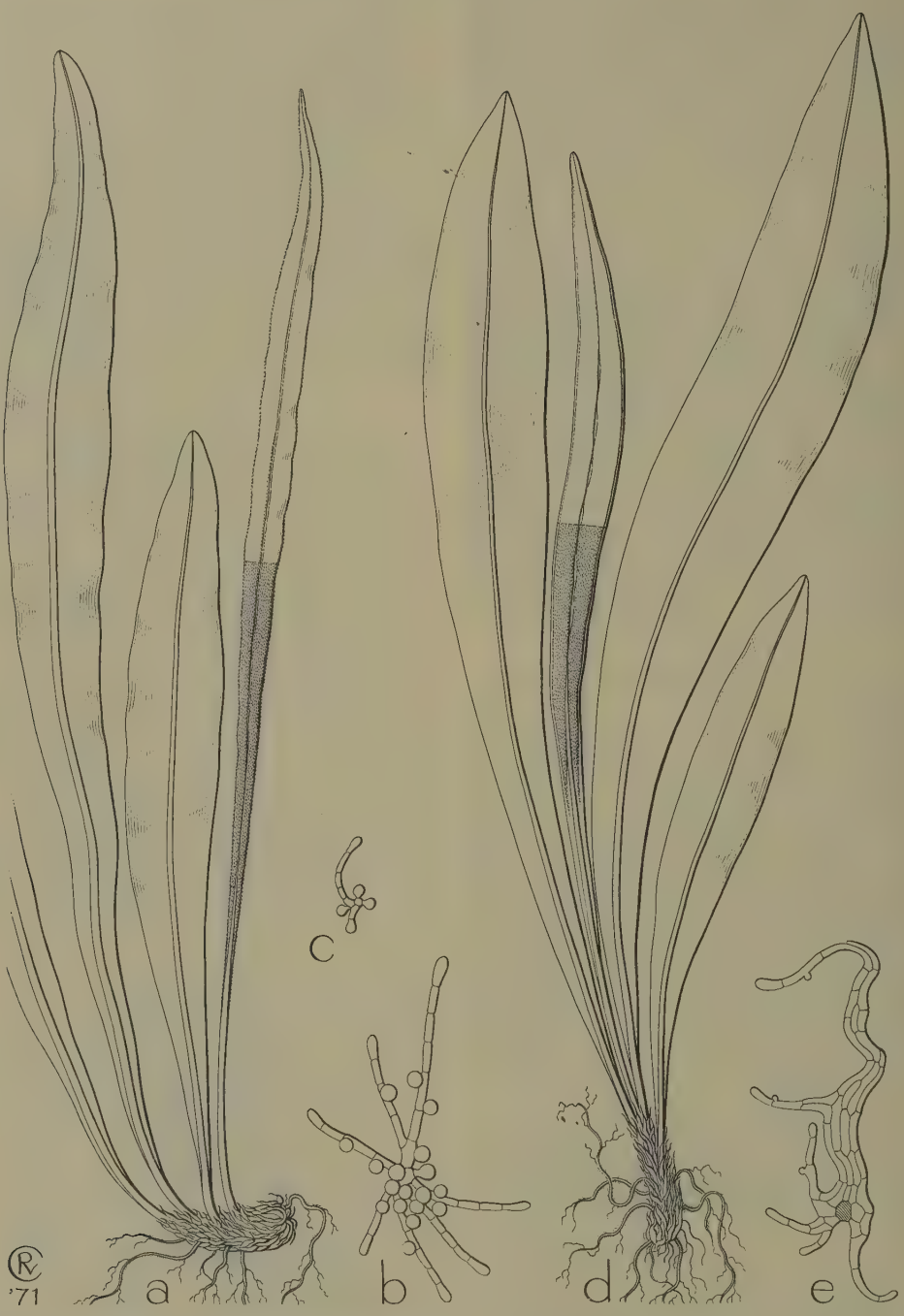

Fig. 18. *Elaphoglossum norrisii* (HOOK.) BEDD. *a*. Plant with 1 fertile and 2 sterile fronds, × 1/2, *b–c*. scales from lower surface of frond, × 40. — *E. melanostictum* (BL.) MOORE. *d*. Plant with 1 fertile and 3 sterile fronds, × 1/2, *e*. scale from lower surface of frond, × 32 (*a* BACKER 10998, *d* RAAP 236).

and dull, with some slender marginal hairs; phyllopodia 1–1$^1/_2$ cm long. *Sterile frond:* stipe to 1$^1/_2$ cm long; lamina rather thick, rigid when dry, to 30 by 5–6 cm, widest above middle, tapering gradually to decurrent base and rather abruptly to broadly pointed or slightly rounded apex; thin pale edge very narrow; veins not distinct; costa beneath broad, slightly prominent; scales on lower surface sparse, stellate, under 1 mm ∅ including rays, with some spherical cells near point of attachment. *Fertile frond:* fertile part of lamina to 18 by 2$^1/_2$ cm, gradually narrowed to base which continues as a sterile wing 10 cm long almost to phyllopodium, apex abruptly narrowed and rounded.

Distr. S. Vietnam; in *Malesia:* Borneo (Sarawak, Sabah), Moluccas (Ceram) (?), W. New Guinea.

Ecol. Epiphyte at 1800–2100 m (1000–1800 m in Vietnam).

Note. Some specimens from S. Vietnam have sterile fronds to 40 cm long and fertile to 20 by 4 cm; I have seen none so large in Malesia, and the above description is mainly from Malesian specimens.

18. Elaphoglossum melanostictum (Bl.) Moore, Ind. Fil. (1862) 361; v.A.v.R. Handb. (1908) 716; Suppl. (1917) 427; Backer & Posth. Varenfl. Java (1939) 249. — *Acrostichum melanostictum* Bl. Fl. Jav. Fil. (1829) 26, t. 7. — Type: van Hasselt, Java (L).

Acrostichum lessonii Mett. in Kuhn, Linnaea 36 (1969) 60, excl. pl. Lesson. — Lectotype: Korthals *s.n.*, Sumatra (B).

Acrostichum beccarianum Baker, Malesia 3 (1886) 27. — *E. beccarianum* C.Chr. Ind. Fil. (1905) 303; v.A.v.R. Handb. (1908) 714. — Type: Beccari *s.n.* Nov. 1865, Kuching, Sarawak (FI; dupl. in K).

E. basilanicum Copel. Philip. J. Sc. 11 (1916) Bot. 41; v.A.v.R. Handb. Suppl. (1917) 425; Copel. Fern Fl. Philip. (1960) 280. — Type: Reillo BS 16232, Basilan (MICH; dupl. in P).

E. peninsulare Holttum, Gard. Bull. S. S. 11 (1947) 270; Rev. Fl. Mal. 2 (1954) 456, f. 266. — Type: Eryl Smith 2021, Patani, Thailand (SING; dupl. in K).

Acrostichum apodum (*non* Kaulf.) Fée, Hist. Acrost. (1845) 42, *pl. jav. tantum.*

Acrostichum norrisii (*non* Hook.) Cesati, Atti Acad. Napoli 7, pt 8 (1876) 31. — **Fig. 18d, e.**

Rhizome short; scales dark brown, to 10 mm long (often shorter), 1 mm wide, acuminate, edges with short stiff hairs; phyllopodia 1–2 cm long. *Sterile frond:* stipe 0–3 cm; lamina thinly coriaceous, to 40 by 6–7 cm, widest $^1/_3$ from apex, narrowed gradually to long-decurrent base, apex broadly but distinctly pointed; thinner edge narrow, not decoloured; veins usually distinct; costa rounded and prominent beneath; scales on lower surface light brown, irregularly stellate with slender arms to 1–1$^1/_2$ mm long, lacking conspicuous spherical cells near point of attachment. *Fertile frond:* stipe 7–15 cm; lamina 11–30 cm long, 1.3–3.7 cm wide, shape as sterile.

Distr. Peninsular Thailand and *Malesia:* Sumatra, Malay Peninsula, Java, Borneo, Philippines (Basilan, Samar, Negros, Mindanao).

Ecol. Epiphytic on tree-trunks in forest at 100–1700 m.

Notes. *E. basilanicum* was described from rather small sterile plants, but in shape of frond and scales agrees closely with other specimens. The species *Acrostichum lessonii* was based in part on specimens collected by Lesson on Vanicoro (Santa Cruz I.) and partly on a specimen from Sumatra, coll. Korthals. The latter alone has a fertile frond, and its sterile ones are much larger than those from Vanicoro. The description agrees with the Sumatran plant, which should thus be the type; the Vanicoro plant is different and I cannot identify it.

A collection of Grabowsky (*s.n.* Jan. 1882; B, BM) from SE. Borneo, is rather intermediate both in scales and frond-form between *E. melanostictum* and *E. norrisii*; sterile fronds to 20 by 3 cm, fertile with long stipe as melanostictum but only 1 cm wide and very long-decurrent. I regard these specimens as small *E. melanostictum.*

19. Elaphoglossum heterostipes Holttum, Blumea 14 (1966) 321. — Type: Endert 4424, Borneo, W. Kutai, Mt Kemul (BO).

Rhizome short; scales medium brown, thin, 5–7 by 1$^1/_2$–2 mm, subentire, apex narrowed but not acuminate; phyllopodia 1 cm long. *Sterile frond:* unwinged stipe 0–5 cm; lamina thinly coriaceous, to 38 by 4.8 cm, widest above middle, base narrowly long-decurrent, apex narrowed to acute (not acuminate) tip; thin edge distinct but not decoloured; costa beneath distinctly prominent; veins slightly prominent on both surfaces, their swollen ends distinct; scales on lower surface numerous, very small, dark, lacking long hairs. *Fertile frond:* stipe 25–30 cm; lamina 25 by 2 cm, shape as sterile.

Distr. *Malesia:* E. Borneo. Only known from type collection.

Ecol. In forest at 1800 m.

Note. This species has sterile fronds closely similar to those of *E. melanostictum* in shape, but differs in scales on rhizome and fronds and in the very long stipe of fertile frond. Endert collected *E. melanostictum* on the same mountain at 1600 m.

20. Elaphoglossum calanasanicum Holttum, Kalikasan, Philip. J. Biol. 3 (1974) 196. — Type: M. G. Price 2933, Luzon, Kalinga-Apayao Prov., Calanasan (K, PNH).

Rhizome short; scales to 15 by 1 mm, brown, glossy, crisped, with few marginal hairs; phyllopodia 1 cm long. *Sterile frond:* stipe to 2 cm; lamina to 34 by 2.7 cm, widest about middle, gradually narrowed to base and more abruptly to acute apex; costa almost flat both sides; veins faintly visible, not prominent; cartilaginous edge hardly $^1/_4$ mm wide. *Fertile frond:* unwinged stipe to 2 cm long, then a narrowly winged portion 7–8 cm long, gradually widening upwards, lamina 12–15 by 2 cm, widest at middle, narrowed about equally to acute apex and to base, scales on upper surface to $^1/_2$ mm long, stellate, end cells of arms ellipsoid.

Distr. *Malesia:* Philippines (Luzon), only known from the type.

Ecol. At 1400 m, abundant, growing with *E. ophioglossoides.*

21. Elaphoglossum norrisii (Hook.) Bedd. Ferns Br. India pt 23 (1870) *addendum*; Handb. Ferns

Br. India (1883) 418; Suppl. (1892) 104; v.A.v.R. Handb. (1908) 716. — *Acrostichum norrisii* HOOK. Spec. Fil. 5 (1864) 215. — *E. melanostictum* [*non* (BL.) MOORE] HOLTTUM, Rev. Fl. Mal. 2 (1954) 455, f. 265. — Type: NORRIS, Penang (K). — **Fig. 18a–c.**

Rhizome short; scales to 10 by $1^1/_2$ mm, rather dark red-brown, thin, tapering to a fine point, edges with irregular teeth and hairs; phyllopodia short. *Sterile frond:* no stipe; lamina 20–40 by 2–4 cm, thinly coriaceous, usually widest above middle, very gradually narrowed to base, more shortly to rather narrow but rounded apex; thin pale edge very narrow; veins faintly visible; costa beneath broad and little prominent; scales on lower surface stellate with short arms and conspicuous spherical cells near point of attachment. *Fertile frond:* stipe commonly to 2 cm, sometimes longer; lamina commonly to 20 by 1 cm, widest seen 1.3 cm.

Distr. *Malesia:* Sumatra, Malay Peninsula, Borneo, W. Java, W. New Guinea.

Ecol. In forest, on mossy tree-trunks and rocks, at 60–1500 m.

22. Elaphoglossum apoense HOLTTUM, Blumea 14 (1966) 320. — Type: EDAÑO PNH 710, Mt Apo, Mindanao (MICH). — **Fig. 20d.**

Rhizome short; scales dark, rigid, glossy, somewhat contorted, 5 by $^1/_2$ mm, hair-pointed with some lateral stiff hairs; phyllopodia 1 cm long. *Sterile frond:* stipe 22 cm long, pale, bearing scales of various sizes from very small to 5 mm long, the latter as those on rhizome but narrower; lamina thinly coriaceous, $19^1/_2$ by 3 cm, widest $^1/_3$ from apex, tapered gradually towards base which is not decurrent, towards apex narrowed a little and then rounded; thin pale edge very narrow; veins distinct; costa prominent and rounded beneath; scales on both surfaces abundant, dark brown, glossy, very narrow, mostly 1–2 mm long, with spreading rigid marginal hairs each consisting of one dark cylindrical cell with a small pale cell at its apex (not seen at × 10 magnification); many scales 1 mm long attached close to edge of lamina and spreading beyond it. *Fertile frond* not seen.

Distr. *Malesia:* Philippines (Mindanao), Papua New Guinea (Mt Albert Edward, T. NAIKAKE 552).

Ecol. In mossy forest, at 2100 m.

23. Elaphoglossum vepriferum HOLTTUM, Blumea 14 (1966) 326. — Type: CLEMENS 7417, NE. New Guinea, Morobe District, Sambanga (B; dupl. in GH sterile).

Rhizome creeping, bearing fronds to 8 mm apart in each rank; scales as in *E. apoense*; phyllopodia 10–15 mm long. *Sterile frond:* stipe 15–25 cm, rather persistently scaly with narrow dark glossy scales to 1 mm long with rigid short marginal hairs; lamina to at least 20 by 2.2 cm, thinly coriaceous, widest above the middle, apex narrowed slightly and rounded, base rather narrowly cuneate, not long-decurrent; pale edge firm, distinct; veins just visible; costa slightly prominent beneath; scales on lower surface of costa dark, very narrow, $^1/_2$–1 mm long, with stiff marginal hairs as in *E. apoense*; smaller paler scales with similar rigid hairs at first abundant on both surfaces, those near edge $^1/_2$ mm long and forming a short tangled fringe spreading beyond edge of lamina. *Fertile frond:* stipe 17 cm; lamina 14 by 1.4 cm, shape as sterile.

Distr. *Malesia:* E. New Guinea. Only known from type collection.

Ecol. In forest, at 1500–1800 m.

24. Elaphoglossum nigripes HOLTTUM, Blumea 14 (1966) 323. — Type: PULLE 493, W. New Guinea, Mt Parameles (BM; dupl. in BO, L, U).

Rhizome creeping, rather slender, fronds close; scales dark, glossy, apparently 3 by 1 mm, not slender-tipped; phyllopodia 5 mm long. *Sterile frond:* stipe 5 cm, covered when young with appressed small dark entire scales; lamina thinly coriaceous, 25–40 by 1.8–$2^1/_2$ cm, widest above middle, very gradually narrowed to decurrent base, also gradually to narrowly rounded apex; thin edge very narrow, reflexed when dry; veins ± distinct; costa slender and prominent beneath; scales on costa beneath small, appressed, ovate-acute, dark, glossy; scales on lamina few, small, dark, appressed, with a few spreading hairs 2–3 cells long. *Fertile frond:* stipe 10 cm; lamina to 25 by 1.3 cm, shape as sterile, with rather abruptly narrowed blunt apex.

Distr. *Malesia:* W. New Guinea. Only known from two collections.

Ecol. In forest, at 1100–2500 m.

25. Elaphoglossum melanochlamys HOLTTUM, Blumea 14 (1966) 322. — Type: EYMA 5408, W. New Guinea, Wissel Lakes (BO; dupl. in L).

Rhizome short; scales mostly black, rigid, glossy, 5 mm long, less than 1 mm wide, acuminate, edges short-toothed or with some stiff hairs; phyllopodia to 1 cm long. *Sterile frond:* stipe 3–5 cm long, pale, rather persistently scaly, scales as rhizome, narrow, spreading, with more conspicuous marginal hairs; lamina rigid, drying rather pale, 15–21 by 1.6 cm, sides parallel for most of length, narrowed rather abruptly to non-decurrent base and to narrowly rounded apex; pale edge distinct, $^1/_2$ mm wide; veins obscure; costa beneath broad, pale, slightly prominent; scales on lower surface abundant, as those on stipe but smaller, mostly 1–3 mm long. *Fertile frond:* stipe 5 cm; lamina 15 by 1.4 cm; abundant scales among sporangia.

Distr. *Malesia:* W. New Guinea. Only known from type collection.

Ecol. Probably at over 2000 m.

26. Elaphoglossum nesioticum HOLTTUM, Blumea 14 (1966) 323. — Type: BRASS 24882, Goodenough I. (A).

Rhizome short; scales dark, glossy, rigid, *c.* 7 mm long, hardly 1 mm wide, somewhat crisped, marginal hairs few; phyllopodia 1 cm long. *Sterile frond:* stipe 6–8 cm; lamina thin, 20–37 by 1–3.8 cm, widest about middle, narrowed gradually to decurrent base and to narrow slightly acuminate apex; thin edge very narrow, deflexed; veins slightly prominent, apices sometimes anastomosing; costa beneath slightly prominent; surfaces glabrescent. *Fertile frond:* stipe 8 cm; lamina 19 by $1^1/_2$ cm, shape as sterile.

Distr. *Malesia:* E. New Guinea (Goodenough I.) (4 collections).

Ecol. Epiphyte in mossy forest, at 1500–1600 m.

27. Elaphoglossum angustifrons HOLTTUM, Blumea 14 (1966) 319. — Type: WOMERSLEY NGF 11272, NE. New Guinea, Minj (LAE; dupl. in A, K).

Rhizome short; scales dark, glossy, flat, to 6 by 2 mm, subentire, not long-acuminate; phyllopodia 2–3 cm long. *Sterile frond:* stipe 5–10 cm, rather pale, at first with spreading scales as rhizome, persistent scales very small, dark brown, entire or with a few hairs; lamina thinly coriaceous, drying dark, 25–35 by $1^1/_2$–2.3 cm, sides parallel for most of their length, base very narrowly cuneate and ± decurrent, apex short-acuminate; thin edge very narrow, not pale; veins distinct, mostly with free thickened tips, occasionally joining near margin; costa pale and prominent beneath; scales persistent on lower surface, very small, dark, with a few short hairs which seem often abraded. *Fertile frond:* stipe 10–15 cm; lamina 16–20 by 1.2–$1^1/_2$ cm.

Distr. *Malesia:* E. New Guinea. Only known from type collection.

Ecol. At 2100–2400 m.

Note. This has the aspect of *E. heterolepium*, but very different scales, and appears to be nearly related to *E. archboldii*.

28. Elaphoglossum pallescens HOLTTUM, Blumea 14 (1966) 323. — Type: BRASS 22879, Papua, Mt Dayman (A).

Rhizome short; scales dark brown, glossy, *c.* 10 by $1^1/_2$ mm, rigid, flat, hair-pointed, with short marginal teeth and slender marginal hairs; phyllopodia 1 cm long. *Sterile frond:* stipe 9–12 cm, pale; lamina rigid, drying pale, to at least 21 cm long, 2.8–4 cm wide, edges parallel in middle part, tapering about equally to slightly acuminate apex and slightly decurrent base; decoloured edge very narrow, reflexed; veins obscure; costa broad and slightly prominent beneath; scales on lower surface dark, appressed, ± stellate with arms of several cells, in all to $^1/_2$ mm wide; upper surface with scattered small pits in which are shrivelled scales. *Fertile frond:* stipe 15 cm; lamina 15 by $2^1/_2$ cm, base rather abruptly narrowed and slightly decurrent.

Distr. *Malesia:* E. New Guinea (2 collections).

Ecol. Low on mossy tree in forest, 1800–2230 m.

29. Elaphoglossum arachnoideum HOLTTUM, Blumea 14 (1966) 320. — Type: BRASS 24541, Goodenough I. (A).

Rhizome short; scales 10 by $1^1/_2$ mm, acuminate, rather dull medium brown, stiff, subentire, somewhat twisted; phyllopodia *c.* 1 cm long. *Sterile frond:* stipe 20 cm, rather persistently scaly as rhizome but scales thinner; lamina firm but rather thin, 21 by 5.8 cm, widest in middle, almost elliptical, base slightly decurrent, apex rounded but not broadly; thin edge not sharply distinct; veins just distinct; costa beneath slightly prominent only near base; lower surface rather persistently scaly, many scales 2–3 mm long, very narrow, pale brown with a few marginal hairs, also abundant much smaller scales; scales near margin a little wider and projecting 2–3 mm, mostly abraded. *Fertile frond:* stipe 22 cm; lamina 12 by 3 cm, shape as sterile.

Distr. *Malesia:* E. New Guinea (Goodenough I.). Only known from type collection.

Ecol. High on trees in oak forest, at 1600 m.

30. Elaphoglossum stenolepis BELL ex HOLTTUM, Blumea 14 (1966) 325. — *E. decurrens* (*non* DESV.) C.CHR. Gard. Bull. S. S. 7 (1934) 290, *p.p.* — Type: CLEMENS 28019, Mt Kinabalu (US).

Rhizome thick, short; scales *c.* 10 mm long, less than 1 mm wide, crisped, red-brown, entire, narrowed to a slender tip; phyllopodia *c.* 1 cm long. *Sterile frond:* stipe 7 cm long, the upper 2 cm narrowly winged; lamina 17–20 by $3^1/_2$–4 cm, rigid, rather thick, drying brown and wrinkled, widest above middle, narrowed gradually to wing at base and to broadly pointed or slightly rounded apex; thin pale edge very narrow; veins obscure; costa beneath broad, pale, little prominent; scales very small, stellate with 3–6 arms of several cells with small glandular cells laterally on arms. *Fertile frond:* stipe 11 cm; lamina 11 by 2.2 cm, rather abruptly narrowed at base and at rounded apex.

Distr. *Malesia:* N. Borneo (Mt Kinabalu), several collections.

Ecol. Epiphyte at 1500–2150 m.

Note. This species grows with *E. annamense*, and CLEMENS 27060 is a mixture of the two species. The scales of *E. stenolepis* are very distinctive, also the longer stipe.

31. Elaphoglossum amblyphyllum BELL, *nom. nov.* — *E. obtusifolium* BELL, Kew Bull. 14 (1960) 83, *non* BRACK. — *Acrostichum decurrens* (*non* DESV.) BL. En. Pl. Jav. (1828) 102; Fl. Jav. Fil. (1829) 32, t. 10; RACIB. Fl. Btzg 1 (1898) 47. — *E. decurrens* (*non* DESV.) v.A.v.R. Handb. (1908) 713, *p.p.*; Suppl. (1917) 424, *p.p.*; BACKER & POSTH. Varenfl. Java (1939) 249; HOLTTUM, Rev. Fl. Mal. 2 (1954) 458, f. 268. — Type: BLUME, Java (L).

Acrostichum obtusifolium (*non* WILLD.) BL. En. Pl. Jav. (1828) 102; Fl. Jav. Fil. (1829) 31; HOOK. Spec. Fil. 5 (1864) 204, *p.p.* — *Olfersia blumeana* PRESL, Tent. Pterid. (1836) 235. — Type: BLUME, Java (L). — **Fig. 19.**

Rhizome short; scales pale brown, 10–12 mm long, to 2 mm wide at base, acuminate, edges ± ciliate; phyllopodia 1 cm long. *Sterile frond:* stipe 7–15 cm long; lamina coriaceous, to 29 by $8^1/_2$ cm, widest above the middle, apex broadly rounded, base cuneate and shortly decurrent; pale edge distinct, narrow; veins obscure; costa beneath broad and little prominent; scales small, appressed, stellate, with some small spherical cells near point of attachment. *Fertile frond:* stipe 20 cm; lamina to 20 by 4 cm.

Distr. *Malesia:* Sumatra, Malay Peninsula, Java, Borneo, Moluccas (Ambon).

Ecol. Epiphyte on old mangrove trees and by rivers, at 0–800 m.

Notes. The type is the specimen illustrated by BLUME as *Acrostichum decurrens*. As shown by BELL (*l.c.* 1960) it is certainly different from the type of *A. decurrens* DESV. The latter is a poor specimen, and I have been unable to identify any Malesian species with it. The specimen named *Acrostichum obtusifolium* WILLD. by BLUME is certainly not conspecific with WILLDENOW's type, which is probably a young plant of *Polypodium scolopendria* BURM. *f.* (photograph seen, showing venation). The name *Elaphoglossum obtusifolium* was published by BRACKENRIDGE with a description of a Fiji specimen, and citation of *Acrostichum obtusifolium* BL. (*non* WILLD.) as a synonym. RACIBORSKI's

description of *Acrostichum decurrens* was based on a specimen from Ambon (leg. TEYSMANN) which I have seen.

Fig. 19. *Elaphoglossum amblyphyllum* BELL. *a.* Habit, 1 fertile and 2 sterile fronds, × 1/2, *b–c.* scales from surface of frond, × 75 (L 908.332–621, 908.352–637).

32. Elaphoglossum luzonicum COPEL. in Elmer, Leafl. Philip. Bot. 1 (1907) 235; *ibid.* 2 (1908) 416; v.A.v.R. Handb. (1908) 714; COPEL. Fern Fl. Philip. (1960) 278. — Type: ELMER 9036 (MICH, *teste* COPEL. MS; dupl. in BO, K, L, P, US).

Acrostichum decurrens var. ornatum FÉE, Hist. Acrost. (1845) 34. — *Acrostichum decurrens* (*non* DESV.) HOOK. Spec. Fil. 5 (1864) 203. — Type: CUMING 144, Luzon (BM, K, L, MICH, P, US).

Acrostichum cumingii (*non* FÉE) BAKER, Syn. Fil. (1868) 407. — *Acrostichum decurrens var. major* METT. *ex* KUHN, Ann. Mus. Bot. Lugd.-Bat. 4 (1869) 292. — *E. decurrens var. cumingii* v.A.v.R. Handb. (1908) 713. — Type: CUMING 193, Luzon (BM, K, P).

E. elmeri COPEL. in Elmer, Leafl. Philip. Bot. 3 (1910) 849; v.A.v.R. Handb. Suppl. (1917) 424; COPEL. Fern Fl. Philip. (1960) 279. — Type: ELMER 11658, Mindanao (not seen).

E. lepidopodum C.CHR. *ex* OGATA, J. Jap. Bot. 13 (1937) 121. — Type: M. OGATA 60, Taiwan, Prov. Taito (BM).

E. cumingii var. papuanum C.CHR. Brittonia 2 (1937) 317. — Type: BRASS 4112, Papua (NY). — **Fig. 20a–c.**

Rhizome short; scales thin, light brown, 5–7 by 2–3 mm, edges with short hairs; phyllopodia to 2 cm long. *Sterile frond:* on young plants widest above middle with ± broadly rounded apex and gradually narrowed base, with a rather persistent fringe of spreading scales 1 1/2–2 mm long all along edge of lamina; lamina to *c.* 20 by 4 cm; on mature plants with stipe 10–15 cm, persistently scaly as rhizome, lamina rigidly coriaceous, to 25 by 3.2–4 1/2 cm, widest at or a little above middle, sides parallel for most of their length, narrowed rather abruptly at both ends, base a little decurrent, apex bluntly pointed or rounded; pale thin edge distinct; veins obscure; costa slightly raised on lower surface; small scales on lamina light brown, to 1 mm long, narrow with hairs near base, near edge of lamina on both surfaces broader scales 1 mm long ± persistent. *Fertile frond:* stipe 17 cm; lamina to 26 by 3 1/2 cm.

Distr. Taiwan; in *Malesia:* Philippines (Luzon, Negros, Panay, Mindanao), E. New Guinea.

Ecol. In mossy forest, at 2000–2300 m (few altitudes recorded).

Notes. The type of *E. luzonicum* cited with the original description was ELMER 8190; but COPELAND wrote "TYPE" on the specimen of *no* 9036 in his own herbarium (MICH) without explaining the discrepancy. I have not seen any specimen bearing the number ELMER 8190.

The treatment of this species (and, with it, that of *E. amblyphyllum*) has been very confused, both taxonomically and nomenclaturally. In his enumeration of CUMING's Philippine ferns, JOHN SMITH cited CUMING 144 and 193 under the name *E. obtusifolium*, based on *Acrostichum obtusifolium* WILLD. citing *A. decurrens* BL. as synonym. But as the generic name *Elaphoglossum* had not then been validly published, the binomial *E. obtusifolium* J.SM. was illegitimate (see p. 314). Further, the type of *Acrostichum obtusifolium* WILLD. is a *Polypodium*-ally; and the specimen described by BLUME as *A. decurrens* does correspond with DESVAUX's type of that species; both epithets will also be found confusedly in the synonymy of *E. amblyphyllum.*

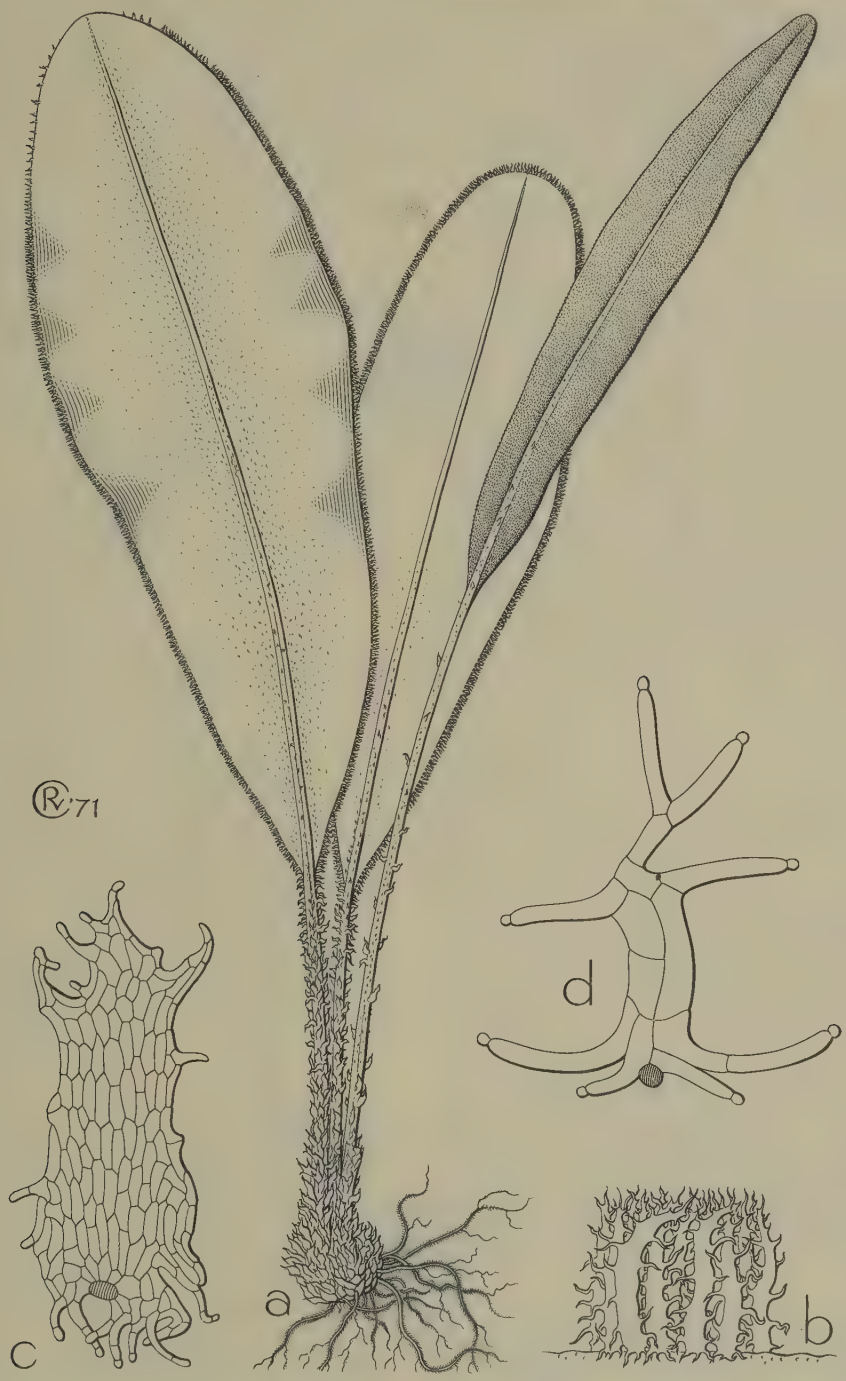

Fig. 20. *Elaphoglossum luzonicum* COPEL. *a*. Habit, × 1/2, *b*. scales on margin of frond, × 10, *c*. scale from margin, × 25. — *E. apoense* HOLTTUM. *d*. Scale from surface of frond, × 75 (*a–b* BS 35595 & a part of ELMER 17489, *d* EDAÑO PNH 710).

Fig. 21. *Elaphoglossum callifolium* (BL.) MOORE. *a*. Habit, 1 sterile and 1 fertile frond, × 1/3, *b*. margin of sterile frond, × 3, *c*. scale from surface of frond, × 50, *d–e*. scales from base of stipe, × 2 (*a–b*, *d* L 908.331–933).

FÉE described his specimen of CUMING 144 as *Acrostichum decurrens var. ornatum*. He cited CUMING 193 as type of *A. cumingii*, but, as noted by COPELAND, his description does not agree with specimens of that collection in other herbaria, and his name is therefore here regarded as doubtful (see p. 314). HOOKER included *A. cumingii* FÉE as one of many synonyms of *A. conforme* SW. (Spec. Fil. 5: 199) citing CUMING 193; but BAKER, in Syn. Fil., recognized *A. cumingii* as a distinct species, basing his description on the specimen of CUMING 193 in HOOKER's herbarium.

In 1960 COPELAND doubted whether his *E. elmeri* and *E. luzonicum* were distinct species. I have examined many specimens of the type collection of *E. luzonicum* and of CUMING 144 and 193. I have come to the conclusion that the type of *E. luzonicum* and CUMING 193 are conspecific. CUMING 144 consists entirely of sterile plants, and I regard these as ± immature stages of the same species as 193; some other collections show intermediate conditions. As in some other species of this genus, young plants have fronds with more broadly rounded apices and more decurrent bases than fronds of mature plants. Fronds of young plants also have a more persistent fringe of scales which are larger than on mature plants; old fronds of some mature plants lack such a fringe, but the scars of attachment of the scales can be seen.

33. Elaphoglossum brevifolium HOLTTUM, Gard. Bull. Sing. 11 (1947) 270; Rev. Fl. Mal. 2 (1954) 458, f. 267. — Type: HOLTTUM 20750, G. Tahan, Malaya (SING; dupl. in K).

Rhizome short; scales rather light brown, thin, *c.* 10 by $1^1/_2$ mm, tapered to a slender apex, entire; phyllopodia 1 cm long. *Sterile frond:* stipe 4–12 cm long, pale, about half of it with a very narrow wing, bearing some residual scales as rhizome; lamina thick and rigid when dry, 8–12 by $3^1/_2$–6 cm, almost elliptical but base decurrent, apex broadly bluntly pointed; thin pale edge $^1/_2$ mm wide, sometimes deflexed on drying; veins obscure; costa beneath slightly prominent in basal half; scales on surfaces at first abundant, very small, with a few marginal hairs of 2–3 cells. *Fertile frond:* stipe 20–25 cm; lamina 8–10 by 2–3 cm, shape as sterile.

Distr. *Malesia:* Malay Peninsula (G. Tahan and G. Batu Puteh).

Ecol. At 1400–1850 m; on G. Tahan a low epiphyte in mossy forest.

34. Elaphoglossum negrosensis HOLTTUM, Blumea 14 (1966) 323. — *E. conforme* [*non* (SW.) J.SM.] COPEL. in Elmer, Leafl. Philip. Bot. 2 (1908) 417. — *E. angulatum* [*non* (BL.) MOORE] COPEL. Fern Fl. Philip. (1960) 278, *p.p.* — Type: ELMER 9885, Philippines, Negros (MICH; BO).

Rhizome short; scales rather light brown, to 7 by $2^1/_2$ mm, acuminate but not hair-pointed, with few marginal hairs; phyllopodia 1 cm long. *Sterile frond:* stipe 2–8 cm, scaly when young as rhizome; lamina thinly coriaceous, 11–17 by 2.7–3.3 cm, widest at or below middle, apex evenly narrowed to a very narrowly rounded tip, hardly acuminate, base rather abruptly narrowed and then decurrent as a wing 2 cm long on the stipe; thin pale edge distinct, less than $^1/_2$ mm wide; veins slender, distinct on both surfaces, rather widely spaced, their apices thickened and not joining; costa hardly prominent on lower surface; no scales seen on lamina. *Fertile frond:* stipe 10–12 cm; lamina 8–11 by 1.3–$1^1/_2$ cm, shape as sterile.

Distr. *Malesia:* Philippines (Negros Oriental). Only known from type collection.

Ecol. In forest, at 1400 m.

Note. The type was originally named *E. conforme* by COPELAND, and later re-named *E. angulatum*, from which it differs in rhizome and vein characters.

35. Elaphoglossum planicosta HOLTTUM, Blumea 14 (1966) 324. — Type: JERMY 4216, NE. New Guinea, Madang Distr., Finisterre Mts (BM).

Rhizome short; scales 10 by 2–$2^1/_2$ mm, narrowed evenly to apex, light brown, thin, with slender marginal hairs; phyllopodia to 1 cm long. *Sterile frond:* stipe pale or slightly rufous, 6–9 (–13) cm long, upper 2–3 cm with narrow wing decurrent from lamina; lamina thick and rigid when dry, 11–15 by 2.7–3.4 cm, widest about middle, rather abruptly narrowed to a ± obtuse-angled apex and more gradually to a narrowly cuneate base; thin pale edge more than $^1/_2$ mm wide; veins obscure except on young fronds, their apices thickened, sometimes forked, the branches then sometimes meeting those of adjacent veins; costa broad, pale, almost flat on lower surface; scales on both surfaces of young fronds appressed, stellate, mostly *c.* $^1/_2$ mm ∅ including arms. *Fertile frond:* stipe 15 cm; lamina 11 by 3 cm, shape as sterile.

Distr. *Malesia:* NE. New Guinea (two collections).

Ecol. In degenerate cloud-forest, epiphytic, at 2750 m.

Note. A fixation from the type collection gave a chromosome count n = *c.* 82 (tetraploid).

36. Elaphoglossum callifolium (BL.) MOORE, Ind. Fil. (1857) 7; CHRIST, Monogr. Elaph. (1890) 34; v.A.v.R. Handb. (1908) 714; Suppl. (1917) 425; C.CHR. Gard. Bull. S. S. 7 (1934) 289; BACKER & POSTH. Varenfl. Java (1939) 251; HOLTTUM, Rev. Fl. Mal. 2 (1954) 459, *p.p.*; COPEL. Fern Fl. Philip. (1960) 277. — *Acrostichum callifolium* BL. En. Pl. Jav. (1828) 100; Fl. Jav. Fil. (1829) 22, t. 4; FÉE, Hist. Acrost. (1845) 28; RACIB. Fl. Btzg 1 (1898) 47. — *Olfersia callifolia* PRESL, Tent. Pterid. (1836) 234. — Type: BLUME, Java (L).

Acrostichum junghuhnianum KUNZE, Bot. Zeit. 6 (1848) 101. — *E. junghuhnianum* MOORE, Ind. Fil. (1857) 10. — Type: JUNGHUHN, Mt Lawu (not seen).

E. reineckei HIERON. & LAUTERB. Bot. Jahrb. 41 (1908) 220. — Type: VAUPEL 452, Samoa (B).

E. permutatum var. mutatum v.A.v.R. Bull. Jard. Bot. Btzg II, 16 (1914) 13; Handb. Suppl. (1917) 426. — Type: RACHMAT 604, Mt Boesoe, Celebes (BO).

E. macgregorii COPEL. Philip. J. Sc. 11 (1916) Bot. 40; v.A.v.R. Handb. Suppl. (1917) 424. — Type: R. C. MCGREGOR BS 19780, Luzon (MICH).

E. laurifolium [*non* (THOUARS] MOORE) v.A.v.R. Handb. (1908) 714, *p.p.*; BACKER & POSTH. Varenfl. Java (1939) 251, *p.p.*

E. commutatum [*non* (METT.) v.A.v.R.] v.A.v.R. Handb. Suppl. (1917) 427, *p.p.* — **Fig. 21, 26f.**

Rhizome massive, fronds close; scales *c.* 10 by 1 mm, rather stiff and straight, often with inflexed edges but not crisped even near apex, entire or nearly so, dull brown; phyllopodia 2–3 cm long. *Sterile frond:* stipe 10–18 cm, rather thick, grooved deeply on upper surface only; lamina coriaceous, commonly to 35 by 5–6 cm, to 48 by 8 cm or more (80 by 10 cm reported in Java), acuminate, base rather narrowly cuneate and a little decurrent; thin edge pale, narrow, usually reflexed when dry; veins distinct but little prominent; costa rounded and prominent beneath; scales on lamina scattered, very small, stellate, brown. *Fertile frond:* stipe usually longer than sterile, to 20 cm or more; lamina commonly to 25 by 4 cm, base rather abruptly narrowed, apex short-acuminate.

Distr. S. Vietnam, throughout *Malesia*; eastwards to Samoa.

Ecol. In mountain forest, sometimes in a dense growth of other epiphytes, at 1000–2400 m.

Notes. There are a few quite small, but fertile, specimens from Java, Sumatra and Borneo which agree so closely with typical *E. callifolium* that I place them here. At least some such have been called *E. laurifolium* (the type of which, from Tristan d'Acunha, is very different in scales) and *E. commutatum*, which see for further comment. But I do not think that the specimen originally named *E. conforme* by BLUME belongs here (see *E. recommutatum*). The Malay Peninsula specimens here described as *E. malayense* have also been called *E. callifolium*, but are very distinct in their scales; I have seen only one Peninsula specimen which seems to be true *E. callifolium*, with a frond 50 by 9 cm.

37. Elaphoglossum commutatum (METT. *ex* KUHN) v.A.v.R. Handb. Suppl. (1917) 427; SLEDGE, Bull. Brit. Mus. (Nat. Hist.) 4 (1967) 90. — *Acrostichum commutatum* METT. *ex* KUHN, Ann. Mus. Bot. Lugd.-Bat. 4 (1869) 292, *excl. spec. Blum.* — *Acrostichum laurifolium* (*non* THOUARS) THW. En. Pl. Zeyl. (1864) 380. — Type: THWAITES 1310 (B; dupl. in K).

E. permutatum v.A.v.R. Bull. Jard. Bot. Btzg II. 16 (1914) 13; Handb. Suppl. (1917) 425, *excl. var. mutatum.* — Type: MATTHEW 696, Mt Sago, Sumatra (BO). — **Fig. 16a.**

Rhizome usually short with close fronds; scales to 10 by $1^1/_2$ mm, medium brown, rather thin, ± crisped throughout but especially towards hair-pointed apices which are often tangled, edges with some spreading hairs; phyllopodia $1–1^1/_2$ cm long. *Sterile frond:* stipe rather slender, 5–15 cm long, rather deeply 3-sulcate almost to base; lamina thinly coriaceous, commonly to 25 by 6 cm, exceptionally to 30 by 9 cm, distinctly elliptic, rather shortly acuminate, cuneate and slightly decurrent at base; thin edge very narrow, often deflexed; veins slender, prominent on both surfaces, not joining at tips; costa prominent on both surfaces, rather deeply grooved on upper; scales brown, stellate, mostly under $^1/_2$ mm in total ∅. *Fertile frond:* stipe sometimes longer than sterile; lamina 12–17 by $1.8–2^1/_2$ cm.

Distr. Ceylon & S. India; in *Malesia:* Sumatra, W. Java, Borneo, New Guinea.

Ecol. In forest, in two cases recorded as terrestrial (MATTHEW reported of the type of *E. permutatum* "in a patch of moist ground in forest"), at 900–1700 m.

Notes. THWAITES 1310 from Ceylon is taken as type, as it is apparent that KUHN's description was made chiefly from it. The BLUME specimen cited is not a good one and the scales are mostly broken; in my opinion it represents a distinct species (*E. recommutatum*).

Below the decurrent base of the lamina of a frond, a distinct groove develops on each side of the median groove; these lateral grooves are on the lines of the decurrent edges of the lamina (v.A.v.R. described the stipe of *E. permutatum* as plurisulcate).

I have wondered whether *E. commutatum* could be an ecologic form of *E. callifolium*, growing in unusually moist shady conditions. But the Malesian specimens here described agree so closely (except that fronds are somewhat larger) with those from Ceylon and S. India, where typical *E. callifolium* is lacking, that I think it right to maintain *E. commutatum* as a distinct species. MATTHEW, who knew *E. callifolium* well in the field, wrote a MS note on his Sumatran specimen of *E. permutatum* "a most distinct species, fully 500 feet below the level of *E. callifolium*".

38. Elaphoglossum malayense HOLTTUM, Blumea 14 (1966) 322. — *E. callifolium* (*non* BL.) HOLTTUM, Rev. Fl. Mal. 2 (1954) 459, *p.p. max.* — Type: HENDERSON 17765, Cameron Highlands, Malaya (K; dupl. in SING).

Rhizome short, thick, scales to 25 by 3 mm, rather light red-brown, flat, firm, acuminate, marginal hairs rare; phyllopodia to $1^1/_2$ cm long. *Sterile frond:* stipe on immature plants short, on mature plants 5–10 cm; lamina rather thinly coriaceous, to 40 by 5 cm, apex rather shortly acuminate, narrowed more gradually to base and then decurrent as a narrow wing 5 cm or more long; thin edge very narrow, reflexed; veins distinct at least on upper surface, hardly prominent; costa prominent on both surfaces; superficial scales not persistent, very small, stellate. *Fertile frond:* stipe 8–15 cm; lamina to 24 by 2.2 cm, base decurrent or not.

Distr. *Malesia:* Malay Peninsula, Borneo.

Ecol. Epiphyte, at 1050–1400 m.

Notes. This species has been called *E. callifolium* but differs strikingly from the typical *E. callifolium* of Java in its much larger flat rhizome-scales and proportionately narrower, more rigid fronds. Fronds on smallish plants mostly have rather short stipes and much-decurrent lamina, and such plants may bear fertile fronds. In the type collection one specimen has a fertile frond with stipe 8 cm and lamina 18 by 2 cm, base narrowly decurrent, the other has stipe 15 cm, lamina 24 by 2.2 cm, base rather abruptly narrowed. The latter also has costa deeply grooved on upper surface and very prominent below, the former has costa shallowly grooved above and not very prominent beneath.

39. Elaphoglossum recommutatum HOLTTUM, *nom. nov.* — *Acrostichum conforme* (*non* SW.) BL. Fl. Jav. Fil. (1829) 23, t. 5. — *Acrostichum aemulum* (*non* KAULF.) BL. En. Pl. Jav. (1828) 101. — Type: BLUME, Java (L; dupl. in P).

Rhizome short; scales *c.* 6 by $2^1/_2$ mm, not long-acuminate, dull medium brown; phyllopodia 1 cm long. *Sterile frond:* stipe 2 cm (type) to 10 cm long; lamina of type 15 by $2^1/_2$ cm, of other specimens to 27 by $4^1/_2$ cm, thinly coriaceous, base cuneate and slightly decurrent, apex shortly acuminate; pale edge narrow, deflexed; veins just distinct; costa somewhat prominent beneath; scales small, stellate, appressed. *Fertile frond:* stipe of type 5 cm, of other specimens to 22 cm; lamina of type 12 by 1.8 cm, of another Java specimen 28 by 2.2 cm, of a Celebes specimen 20 by $3^1/_2$ cm.

Distr. *Malesia:* Sumatra, Java, SW. Celebes.

Notes. KUHN cited BLUME's specimen under *Acrostichum commutatum* METT., but he evidently described the scales of *A. commutatum* from the Ceylon specimen of THWAITES, as *longe acuminatis*, adding parenthetically (*apice denique delapsis*) an apparent reference to the BLUME specimen, the scales of which are mostly broken. But I judge from BLUME's drawings of the scales, and from another Java specimen (LOBB *s.n.*, K) that the scales are very different from those of the THWAITES specimen; see further comment under *E. commutatum*.

E. recommutatum appears to be the Malesian species nearest to *E. conforme* (SW.) MOORE, type species of the genus. It differs from typical *E. conforme* in the short-acuminate frond-apices and in lacking the resin-spots which occur abundantly on the lower surface of that species.

40. Elaphoglossum sordidum CHRIST, Nova Guinea 8 (1909) 156; v.A.v.R. Handb. Suppl. (1917) 425; COPEL. Philip. J. Sc. 78 (1949) 404. — Type: VERSTEEG 1432, W. New Guinea (BO). — **Fig. 22.**

Rhizome short; scales medium brown, thin, to 6 by 2 mm, acuminate, with many spreading marginal hairs; phyllopodia 1 cm long. *Sterile fronds:* stipe pale, 10–12 cm long, rather persistently scaly, scales narrow; lamina thinly coriaceous, 20–30 by $3^1/_2$–$4^1/_2$ cm, narrowly elliptical, base gradually long-decurrent, apex more shortly acuminate; thin pale edge narrow, deflexed; veins distinct, slightly prominent; costa prominent, slender and terete on lower surface; scales on lower surface appressed, narrow, to 1 mm long, with long marginal hairs. *Fertile fronds:* stipe 12–18 cm; lamina 13–25 by 1–3 cm.

Distr. *Malesia:* W. New Guinea (4 collections).

Ecol. Epiphyte, at 250–780 m.

41. Elaphoglossum novoguineense ROSENST. in Fedde, Rep. 10 (1912) 341; v.A.v.R. Handb. Suppl. (1917) 423; COPEL. Philip. J. Sc. 78 (1949) 404. — Type: BAMLER S.67, NE. New Guinea, Sattelberg (not seen).

E. brassii C.CHR. Brittonia 2 (1937) 316. — Type: BRASS 5558, Mafulu, Papua (NY).

Rhizome short; scales rather thick, dull medium brown, *c.* 5–10 by $2^1/_2$ mm, subentire or sparsely hairy, tapering evenly from base to acute apex; phyllopodia 1–$1^1/_2$ cm long. *Sterile frond:* stipe 4–11 cm long; lamina thinly coriaceous, 20–33 by 2.8–4 cm, widest about middle, base gradually narrowed and decurrent for 2–3 cm, apex acute to acuminate; pale edge narrow, reflexed; veins often slightly prominent; costa rather broad and pale beneath, only slightly prominent; scales small,

Fig. 22. *Elaphoglossum sordidum* CHRIST. *a.* Habit, 2 sterile fronds, 1 fertile frond, × $^1/_3$, *b–c.* scales from base of stipe, × 3 (*a* fertile, *b* BRASS 23000, *a* sterile, *c* BRASS 11498).

stellate. *Fertile frond:* stipe 10–16 cm; frond 15–20 by 1.2–2 cm.

Distr. *Malesia:* New Guinea.

Ecol. Epiphyte, at 1200–2400 m.

Notes. I have examined a KEYSSER specimen (S-PA) from the type locality named and distributed by ROSENSTOCK. The type of *E. brassii* is smaller than above described, with sterile lamina 15 by 3 cm, fertile 7 by 1 cm, but agrees in scaliness. One specimen collected in NE. New Guinea by T. G. WALKER (8155) gave a chromosome count n = *c.* 82 (tetraploid).

42. Elaphoglossum robinsonii HOLTTUM, *sp. nov.*

Paleis pallidis tenuibus integris stipitibusque longis frondium fertilium cum E. brevifolio HOLTTUM (sp. 33) congruens, ab eo differt frondibus multo majoribus, fertilibus sterilibus aequilatis, sporisque multialatis.

Rhizome short; scales to 15 by 2 mm, light brown, thin, flat, margins entire, tapering to apex but not hair-pointed; phyllopodia $1^1/_2$ cm long. *Sterile frond:* stipe to 12 cm long, scaly when young; lamina to 28 by $4^1/_2$ cm, widest at middle and gradually narrowed to both ends, apex broadly pointed (less than 90°), base narrower and slightly decurrent; midrib slightly prominent on lower surface near base, distally almost flat, more prominent and grooved on upper surface; cartilaginous edge less than $^1/_2$ mm wide, reflexed when dry, lacking scales; scales on lower surface of lamina stellate, to *c.* $^1/_2$ mm diameter, with a few short rays. *Fertile frond:* stipe to 24 cm long; lamina to 25 by $4^1/_2$ cm, sides almost parallel for much of their length, base rather broadly cuneate and slightly decurrent, apex broadly pointed; spores bearing numerous small translucent wings.

Type: H. C. ROBINSON, Jan. 1913, Gunong Mengkuang, Selangor, Malaya (K).

Distr. Only known from the type and A. G. PIGGOTT 1093, 1094, from the neighbouring mountain, G. Ulu Kali, at 1500–1800 m.

Note. This species differs from *E. malayense* HOLTTUM, the common species on the Main Range in Malaya, in thinner paler scales, less decurrent base of sterile frond and longer stipe of fertile fronds.

43. Elaphoglossum favigerum HOLTTUM, Blumea 14 (1966) 321. — Type: BRASS 13440, W. New Guinea, near Idenburg River (GH; MICH).

Rhizome short; scales dull dark brown, to *c.* 8 by $1^3/_4$ mm, rather thin, not acuminate, cells ± hexagonal, isodiametric, edges with a few long hairs; phyllopodia *c.* $1^1/_2$ cm long. *Sterile frond:* stipe 10–16 cm; lamina thinly coriaceous, to 39 by $4^1/_2$ cm, widest at middle or below it, base cuneate and slightly decurrent, apex gradually narrowed, acute; thin edge narrow, reflexed, hardly decoloured; veins distinct on upper surface; costa beneath prominent; scales on lower surface minute, slightly stellate or not. *Fertile frond:* stipe 14–16 cm; lamina to 22 by $2^1/_2$ cm, base rather abruptly narrowed, more gradually to acute apex.

Distr. *Malesia:* W. New Guinea (3 collections).

Ecol. Occasional low epiphyte, 1200–1500 m.

44. Elaphoglossum sumatranum HOLTTUM, Blumea 14 (1966) 325. — Type: MATTHEW *s.n.*, 21 Jan. 1913, Sumatra, G. Tandikat (K).

Rhizome short; scales pale brown, rather thin, to 10 by $2^1/_2$ mm, tapering to apex, subentire; phyllopodia 1 cm long. *Sterile frond:* stipe 5–8 cm, pale, bearing scales as rhizome but smaller; lamina 20–30 by $3^1/_2$–5 cm, thick, rigid, drying green, widest at or a little above middle, base gradually or rather abruptly narrowed and slightly decurrent, distally narrowed rather abruptly to rounded apex; edge thick and pale; veins obscure; costa pale, slightly prominent beneath; scales on lower surface small, stellate. *Fertile frond:* stipe 15–20 cm; lamina 14–17 by 1.8–3.3 cm; spores 52–59 by 33–37 μm, with broad perispore having very few folds in it.

Distr. *Malesia:* Central Sumatra (two collections).

Ecol. Epiphyte, at 1500 m.

45. Elaphoglossum indrapurae HOLTTUM, Blumea 14 (1966) 321. — Type: ALSTON 14275, Central Sumatra, near G. Kerintji, Sg. Tandok, Kayu Aro Estate (BM).

Similar to *E. sumatranum* in rhizome-scales and spores, but with thinner, much longer fronds. *Sterile frond:* stipe 14–18 cm; lamina 35–55 by 3–5 cm, thinly coriaceous, base cuneate and slightly decurrent, gradually narrowed distally to narrowly rounded apex; pale edge thin, narrow, deflexed; veins distinct and slightly prominent on upper surface. *Fertile frond:* stipe 38 cm; lamina 33 by 3 cm, base decurrent to a narrow wing 3 cm long.

Distr. *Malesia:* Central West Sumatra. Only known from type collection.

Ecol. In forest, at 1500 m.

Note. This is closely related to *E. sumatranum*, and was collected in the same region, but is so much larger that I think it should stand as a distinct species. It should be noted that ALSTON also collected typical *E. sumatranum*, and no intermediates between the two have been found.

46. Elaphoglossum spongophyllum BELL *ex* HOLTTUM, Blumea 14 (1966) 325. — Type: CLEMENS 31869, N. Borneo, Mt Kinabalu, Upper Kinataki R. (BO).

Rhizome short; scales to 15 by $2^1/_2$ mm, acuminate, rather thin, flat, pale when young, later red-brown, edges with a few hairs; phyllopodia $1^1/_2$–2 cm long. *Sterile frond:* stipe 8–15 cm long, pale; lamina thick, rigid, light brown when dry, to 33 by 7 cm, widest at or above middle, base rather narrowly cuneate, little decurrent, towards apex ± abruptly narrowed to a rounded tip; pale edge thin, very narrow; veins obscure; costa beneath broad, pale, little prominent; scales on lower surface with very small dark centre and 2–4 slender radiating arms. *Fertile frond:* stipe 15 cm; lamina 20–25 by $3^1/_2$–4 cm, widest above middle, base rather narrowly cuneate, apex abruptly narrowed to a narrowly rounded tip; spores *c.* 37 μm long, with much-folded perispore.

Distr. Hainan; in *Malesia:* Malay Peninsula, N. Borneo (Mt Kinabalu).

Ecol. Epiphyte, at 2150–2920 m in N. Borneo, 1550–1850 m in Malaya.

Notes. The only Malayan specimen is from G. Tahan. The Hainan specimen (MCCLURE 20066) was distributed as *E. austrosinicum* MATT. & CHR., which has acuminate fronds much more

decurrent at the base. *E. spongophyllum* has somewhat the same shape of frond as *E. sumatranum*, but it always dries brownish, and the spores are very different.

47. Elaphoglossum blumeanum (FÉE) J.SM. Ferns Brit. & For. (1866) 106. — *Acrostichum blumeanum* FÉE, Hist. Acrost. (1845) 62, *excl. syn. Olfersia blumeana* PRESL. — Type: CUMING 194, Luzon (P; dupl. in US).

E. copelandii CHRIST, Philip. J. Sc. 2 (1907) Bot. 176; v.A.v.R. Handb. (1908) 717; COPEL. Fern Fl. Philip. (1960) 277. — Type: COPELAND 1541, Mindanao (P; dupl. in B, US).

Acrostichum viscosum (*non* SW.) BL. Fl. Jav. Fil. (1829) 27; RACIB. Fl. Btzg 1 (1898) 46.

E. petiolatum [*non* (SW.) URB.] v.A.v.R. Handb. (1908) 717; Suppl. (1917) Corr. 29; BACKER & POSTH. Varenfl. Java (1939) 250.

E. yunnanense [*non* (BAKER) C.CHR.] HOLTTUM, Rev. Fl. Mal. 2 (1954) 455, f. 264. — **Fig. 23a–f.**

var. **blumeanum.**

Rhizome creeping, 3–5 mm ∅ when dry, bearing fronds close together or to 1 cm apart in each of two ranks; scales *c.* 5 mm long, $^1/_2$ mm wide, dark brown, glossy, rigid, acuminate, ± contorted with inrolled edges which bear a few teeth or stiff hairs; phyllopodia to 8 mm long. *Sterile frond:* stipe 12–30 cm long, near base with dark spreading scales as rhizome but often with numerous stiff marginal hairs, rest of stipe ± persistently covered with small stellate scales; lamina to 50 by $3^1/_2$ cm, rather thin, base rather narrowly cuneate, apex acuminate; thin pale edge very narrow; veins slightly prominent on lower surface; costa beneath rounded, prominent; scales on upper surface soon abraded, thin, pale, appressed, ± circular with rather long slender marginal hairs appressed to surface; scales on lower surface rather persistent, very small but with 3–5 stiff marginal hairs to almost 1 mm long spreading away from surface, on old fronds often abraded but leaving resin-dots at points of attachment. *Fertile frond:* stipe 20–35 cm; lamina to 30 by 1.4 cm.

Distr. *Malesia:* Sumatra, Malaya, Java, Borneo, Celebes, Philippines.

Ecol. Epiphyte at 700–2000 m, fronds pendulous.

var. **philippinense** CHRIST MS, *var. nov.* — Type: ELMER 6509, Baguio, Luzon (P; dupl. in B, MICH).

Cum varietate typica squamulis rhizomatis frondisque congruente, differt: frondibus multo minoribus; stipite frondis sterilis 4–6 cm longo, lamina ad 15 × 1.5 cm; stipite frondis fertilis 10–18 cm longo, lamina 5–12 cm × 6–8 mm.

Distr. *Malesia:* Philippines (Luzon). Several collections.

Notes. The name *E. blumeanum* was published by JOHN SMITH in his list of CUMING's Philippine ferns, with a reference to *Acrostichum viscosum* BL. *non* SW.; but as the generic name *Elaphoglossum* had not then been validly published JOHN SMITH's new name was illegitimate. FÉE was the next author to publish the epithet *blumeanum* for this species; he referred to J. SMITH (the illegitimate publication of 1841) but not to BLUME, and described and cited CUMING 194 only, for which reason the CUMING specimen must be the type of *Acrostichum blumeanum* FÉE.

This species is nearly allied to *E. petiolatum* (SW.) URB. of the West Indies. There are also closely allied forms in Africa and the Mascarene Is. (*E. salicifolium* (WILLD. *ex* KAULF.) ALSTON) and India (*Acrostichum stelligerum* WALL. *ex* BAKER), and it would be possible to regard all as varieties of one species. *E. blumeanum* is however larger than the others, and appears to have a greater difference between scales of the upper and lower surfaces, the latter being especially distinctive. The name *E. yunnanense* (BAKER) C.CHR. is probably to be regarded as synonymous with *Acrostichum stelligerum*; the latter epithet has priority but has not yet been formally transferred to *Elaphoglossum*.

48. Elaphoglossum miniatum (CHRIST) CHRIST, Monogr. Elaph. (1899) 72, f. 30; v.A.v.R. Handb. (1908) 716. — *Acrostichum miniatum* CHRIST, Verh. Nat. Ges. Basel 11 (1895) 254, t. 3, f. 25–27; Ann. Jard. Bot. Btzg 15 (1898) 175. — Type: SARASIN 954, Central Celebes (BAS). — **Fig. 23g–j.**

Rhizome and scales as *E. blumeanum*. *Sterile frond:* stipe 7 cm or more, bearing spreading scales 2–3 mm long, paler than on rhizome and with many stiff marginal hairs, also many appressed orbicular ciliate scales; lamina to 25 by $2^1/_2$ cm or more, shape as *E. blumeanum*; scales on upper surface very pale, flat, appressed, ± circular with fringe of pale hairs shorter than width of scale, close to edge of upper surface a fringe of similar but elongate scales (1 mm long) spreading at right angles to edge of lamina and beyond it; scales on lower surface red-brown, a little smaller than those on upper surface, with inflexed edges bearing thicker much longer stiff hairs (to $^1/_2$ mm long). *Fertile frond:* stipe 15 cm or more; lamina to 30 cm long, hardly 1 cm wide.

Distr. *Malesia:* Celebes (two collections); New Guinea (?).

Ecol. At *c.* 1000 m altitude.

Note. Some New Guinea specimens seem somewhat intermediate between this species and *E. heterolepium* as regards scales on the lower surface, but the types of the two species (both from Celebes) are very distinct.

49. Elaphoglossum heterolepium v.A.v.R. Bull. Jard. Bot. Btzg II, 16 (1914) 13; Handb. Suppl. (1917) 426. — *E. petiolatum* (SW.) URBAN, *var.*, C.CHR. Gard. Bull. S. S. 7 (1934) 291. — Type: RACHMAT 522, *partim*, Central Celebes (BO). — **Fig. 23k–m, 24.**

Rhizome and scales as *E. blumeanum*. *Sterile frond:* stipe to 20 cm or more long; lamina light green when fresh, drying dark, thin, 25–45 by 2–2.7 cm, apex acuminate, base more abruptly narrowed and slightly decurrent; thin edge narrow, reflexed; veins distinct; costa rounded and prominent beneath, bearing some dark appressed scales; scales on upper surface pale, thin, flat, circular, short-ciliate, those near edge of lamina sometimes spreading a little beyond the edge; scales on lower surface often (always?) peltate, similar in shape to those of upper surface but firmer and more persistent, when dry with edges turned away from lamina-surface, thus ± cup-shaped. *Fertile frond:*

Fig. 23. *Elaphoglossum blumeanum* (FÉE) J. SM. *a*. Habit, × 1/3, *b–c*. scales of upper surface of frond, × 20, *d*. scales of lower surface , × 20, *e*. scale from stipe, × 7, *f*. edge of sterile frond. — *E. miniatum* (CHRIST) CHRIST. *g*. Scale from upper surface of frond, × 20, *h*. marginal cells of *g*, × 65, *i*. scale from edge of upper surface, × 20, *j*. scale from lower surface, × 20. — *E. heterolepium* v.A.v.R. *k*. Habit, × 1/3, *l*. scale from upper surface of frond, × 30, *m*. scale from lower surface, × 30 (*a–f* L 908.329–719, *g–j* SARASIN 954, *k* NGF 19082, *l–m* CLEMENS 29064).

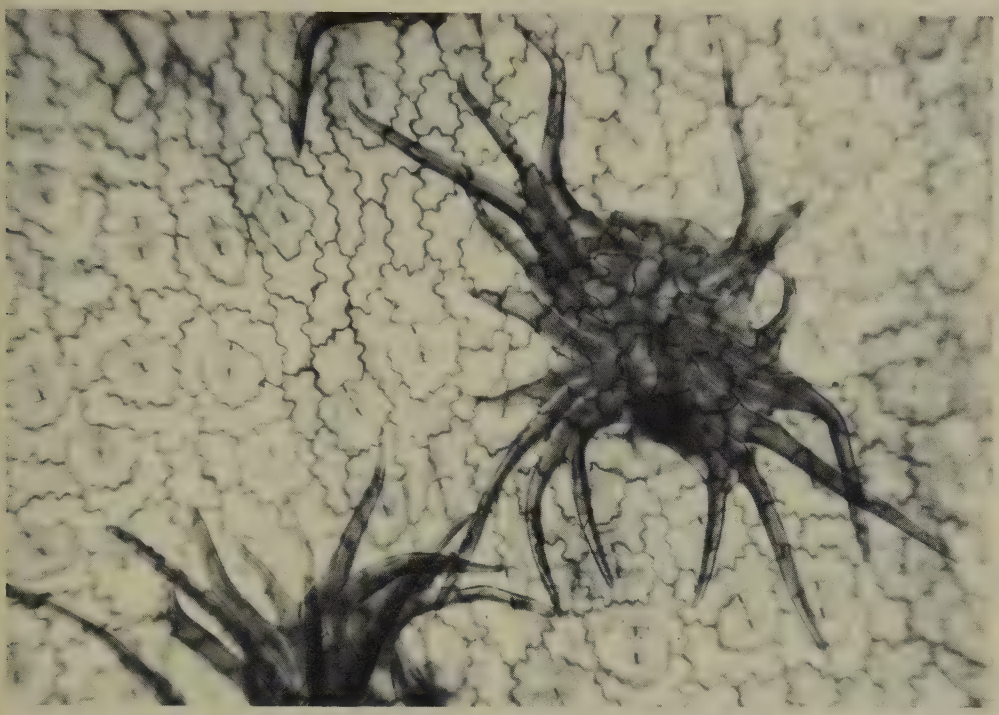

Fig. 24. *Elaphoglossum heterolepium* v.A.v.R. Lower surface of frond, showing scales and cells of epidermis, × 175.

stipe somewhat longer than sterile; lamina 15–30 cm long, 9–15 mm wide.

Distr. *Malesia:* N. Borneo, Celebes, New Guinea.

Ecol. Epiphyte or on rocks, at 1000–2300 m.

Note. The type does not include a fertile frond; with it in the same collection are two fronds of *E. blumeanum*, which appears usually to occur at lower altitudes than *E. heterolepium* in Borneo and Celebes.

50. Elaphoglossum resiniferum HOLTTUM, Blumea 14 (1966) 324. — Type: WAKEFIELD 1466, Papua, Central Division, Astrolabe Range (BM).

Rhizome creeping, 4–5 mm ∅, bearing fronds close together; scales dark brown, glossy, 2–3 mm long, not acuminate, somewhat crisped; phyllopodia less than 5 mm long. *Sterile frond:* stipe 5–7 cm long, pale, almost covered with appressed broadly ovate subentire brown scales less than 1 mm long; lamina thinly coriaceous, 20–26 cm long, 8–9 mm wide, widest about middle, narrowed gradually to decurrent base and caudate apex; edge reflexed and inrolled when dry; veins distinct on lower surface; costa rounded and raised beneath; scales on upper surface of costa as stipe but with short marginal projections of one cell; on upper surface of lamina few persistent scales, same shape as on costa but thin, pale, with short marginal unicellular hairs; on lower surface many small spots of dark reddish resin, apparently on sites of former scales. *Fertile frond:* stipe 11 cm; lamina 18 cm by 7 mm, widest above middle, base gradually and narrowly decurrent, apex not caudate.

Distr. *Malesia:* E. New Guinea. Only known from type specimen.

Ecol. On wet rocks in creek bed, at 2400 m.

Species not occurring in Malesia

Elaphoglossum conforme (SW.) J. SMITH in Hook. J. Bot. 4 (1841) 148. — *Acrostichum conforme* Sw. Syn. Fil. (1806) 10, 192.

This species is confined to St Helena (type) and South Africa. The name has been used confusedly for species in various other parts of the world, including Malesia; HOOKER cited *Acrostichum angulatum* BL. as a synonym of *A. conforme*. See *E. recommutatum*, *no* 38, *supra*.

Elaphoglossum gorgoneum (KAULF.) BRACK. in Wilkes, U.S. Expl. Exp. 16 (1854) 74. — *Acrostichum gorgoneum* KAULF. En. Fil. Chamisso (1824) 63.

This species is confined to Hawaii. The specimen described and figured as *A. gorgoneum* by BLUME (Fl. Jav. Fil. 28, t. 8) is *E. angustatum* (SCHRAD.) HIERON. of South Africa. BLUME's specimen (L) was presumably collected at the Cape by someone travelling to Java, and later mixed with others collected in Java (other examples of this are cited by BACKER & POSTHUMUS, Varenfl. Java p. 144).

BLUME's specimen was subsequently re-named *Acrostichum conforme var. javanicum* by METTENIUS (Ann. Mus. Bot. Lugd.-Bat. 4, (1869, 292). The references to *E. gorgoneum* by v.A.v.R. (Handb. 712, Suppl. 423) are based partly on BLUME, partly on *E. pellucido-marginatum* CHRIST.

Elaphoglossum hirtum (SW.) C.CHR. Ind. Fil. (1905). — *Acrostichum hirtum* SW. in Schrad. J. Bot. 1800/2 (1801) 10. — *Acrostichum squamosum* SW. *non* CAV.

A West Indian species. BEDDOME gave the name *E. squamosum* to plants from S. India and Ceylon, and included Sumatra in the distribution of the species (BEDD. Handb. 420); this statement was copied, under the name *E. hirtum*, by v.A.v.R. (Handb. 717), but I have seen no specimens of the Indian species from Sumatra and do not know the origin of BEDDOME's statement.

Elaphoglossum latifolium (SW.) J.SM. Lond. J. Bot. (1842) 197. — *Acrostichum latifolium* SW. Prodr. (1788) 128.

A tropical American species, described originally from Jamaica. BEDDOME (Handb. 416) so named plants of *E. angulatum* (BL.) MOORE in Ceylon and S. India which he had previously called *E. laurifolium*.

Elaphoglossum laurifolium (THOUARS) MOORE, Ind. Fil. (1857) xvi. — *Acrostichum laurifolium* THOUARS, Fl. Tristan d'Ac. (1804) 31.

Confined to Tristan d'Acunha. The use of this name for species in other parts of the world has caused much confusion; in Malesia the species *E. angulatum* and *E. commutatum* have been so named. BACKER & POSTHUMUS (Varenfl. Java p. 251) have cited *Acrostichum gorgoneum* BL. and several other species as synonyms of *E. laurifolium*.

Elaphoglossum pellucidum GAUD. in Vaillant, Voy. Bonite Bot. Atlas (1844) t. 79, f. 5; MORTON, Contr. U.S. Nat. Herb. 38 (1967) 44. — *Acrostichum micradenium* FÉE, Hist. Acrost. (1845) 43, t. 8, f. 1. — *E. microphyllum* v.A.v.R. Bull. Dép. Agr. Ind. Néerl. 18 (1908) 35; BACKER & POSTH. Varenfl. Java (1939) 249.

E. pellucidum is a Hawaiian species. The type of *E. microphyllum* is a specimen (now in Herb. BO) from the herbarium of Dr PLOEM, who lived in Java for thirty years. The specimen bears no original label; the label written at the time of acquisition at Bogor bears the locality Java, probably on the assumption that all PLOEM's specimens were collected in Java. Other specimens from PLOEM have also been shown to bear incorrect localities (see Cyclopaedia of Collectors, Fl. Males. I, 1, 1950, xxviii, 409).

Doubtful species

Acrostichum cumingii FÉE, Hist. Acrost. (1845) 34.

FÉE cited CUMING 193 as type, but his description differs considerably from all specimens of CUMING 193 which I have seen (BM, K, P, US) in scales and in size and shape of fronds; as COPELAND has stated (Fern Fl. Philip. p. 278) FÉE's description would better fit *E. callifolium*. The specimen from which FÉE prepared his description has not been found at Paris. I therefore regard FÉE's name as of doubtful application, and have referred all specimens of CUMING 193 which I have seen to *E. luzonicum* COPEL.

Acrostichum decurrens DESV. Berl. Mag. 5 (1811) 310.

The type of this species is at Paris. BELL reported upon it in some detail (see *E. amblyphyllum supra, no* 30) and showed that it is not conspecific with the Java species so named by BLUME. I have also examined the specimen, which consists of small detached fronds, lacking rhizome. Its origin is described as Ind. or. I cannot identify it with any of the Malesian species of *Elaphoglossum* here described, and the specimen is so unsatisfactory that I would prefer to regard the name *E. decurrens* DESV. as a *nomen dubium*.

Excluded

Elaphoglossum borneense (BURCK) C.CHR. Ind. Fil. (1905) 303. — *Acrostichum borneense* BURCK, Ann. Jard. Bot. Btzg 4 (1884) 99 = *Syngramma borneensis* (HOOK.) J.SM. (*Gymnogramma borneensis* HOOK.).

It is to be noted that the species of BURCK and HOOKER were based on different types, but they are undoubtedly conspecific.

Names which should not be recognized

JOHN SMITH regarded the generic name *Elaphoglossum* as having been published by SCHOTT in 1834, but as SCHOTT gave no description the publication has no status according to the present Code. The first publication of the name with a description was by SMITH himself, in Aug. 1841. But a few months previously JOHN SMITH had published two new binomials, transferring species from the genus *Acrostichum* to *Elaphoglossum*. These two binomials are therefore now regarded as *nomina nuda*, but they have been recognized by some authors, owing to the fact that the invalidity of SCHOTT's name has only recently been noticed (it was considered valid by CHRISTENSEN, in Index Filicum). These names are therefore cited below, to indicate their status.

Elaphoglossum blumeanum J.SM. in Hook. J. Bot. 3 (May 1841) 401, *nom. nud.*

Elaphoglossum obtusifolium J.SM. *l.c.*, *nom. nud.*

6. BOLBITIS[1]

SCHOTT, Gen. Fil. (1835) *ad t.* 13; C.CHR. Ind. Fil. Suppl. 3 (1934) 102; BACKER & POSTH. Varenfl. Java (1939) 80; COPEL. Gen. Fil. (1947) 115; HOLTTUM, Ferns

(1) Treatment by E. Hennipman, Leyden.

Malaya (1954) 461; COPEL. Fern Fl. Philip. (1960) 254; HENNIPMAN, Leid. Bot. Ser. 2 (1977) 123, *with full synonymy.*

Egenolfia SCHOTT, Gen. Fil. (1835) *ad t.* 16; BACKER & POSTH. Nat. Tijd. N. I. 93 (1933) 152; Varenfl. Java (1939) 84; HOLTTUM, Ferns Malaya (1954) 459; COPEL. Fern Fl. Philip. (1960) 265. — *Polybotrya sect. Egenolfia* DIELS in E. & P. Nat. Pfl. Fam. 1 (1900) 195; v.A.v.R. Handb. Mal. Ferns (1908) 722.

Campium PRESL, Tent. Pterid. (1836) 238, pl. 10 (22–23); COPEL. Philip. J. Sc. 37 (1928) 341, *p.p.*; BACKER & POSTH. Nat. Tijd. N. I. 93 (1933) 157, *p.p.*

Edanyoa COPEL. Philip. J. Sc. 81 (1952) 22, pl. 17. — **Fig. 25, 26a–c, 27–33.**

Rhizome creeping or low-climbing, unbranched or with accessory branches dorsally (and laterally), with 2–6 rows of fronds, ventrally (and laterally) with roots; scales ± appressed, pseudo-peltate, triangular from a perfoliate or subcordate base, up to 15 mm long, usually subclathrate, sometimes (in *B. sinuata*) ± opaque, with sparsely set, slender, uniseriate, thin-walled glandular hairs; vascular system dorsiventric, with a broad gutter-shaped ventral bundle and 1–3 (in *B. heteroclita* rarely up to 4) dorsal bundles (fig. 25d). *Fronds* usually close together, in *B. heteroclita* sometimes spaced; petiole (long-) decurrent on the rhizome, near the lamina base with 1(–3) median and on either side a lateral longitudinal ridge (fig. 25e), aerophores linear, pale, present laterally on either side and especially conspicuous in the basal part of young fronds, in cross-section near the base with a ± U-shaped arrangement of 3–16 vascular bundles of which the two anterior ones are largest. *Sterile fronds* simple or (bi)pinnate with the pinnae alternate or ± opposite and usually continuous with the rachis, in some species ± subarticulate, the two lowermost pinnae usually conform to the other pinnae, sometimes deltoid, sessile or shortly petiolulate, usually herbaceous, sometimes coriaceous, with usually one, rarely more subterminal or terminal bulbils, surface when young apart from scales densely set with uniseriate glandular hairs; *venation pattern:* veins free (*ser. Egenolfianae*) or variously anastomosed and with or without included free veins in the areoles. *Fertile fronds* of similar shape as the sterile ones though with a proportionally larger petiole and a smaller lamina, usually completely acrostichoid, sometimes pteridoid or moniliform; spores with a thin exospore and a variously shaped perispore (fig. 26a–c). — Chromosomes n = 41, 82; 2n = 82, 123.

Distr. Pantropic. In my monograph (*l.c.*) I recognized 44 species arranged in 10 series (of which only *ser. Bolbitianae* is pantropic): Africa incl. Madagascar: 9 *spp.*, America: 14 *spp.*, Asia and the Pacific: 21 *spp.* of which 12 in *Malesia*, Australia (Queensland): 3 *spp.*

Fossils. No fossils can be attributed to the genus. *B. coloradica* R. W. BROWN from the Cretaceous has now been recognized by REVEAL *et al.* (Bringham Young Univ. Geol. Stud. 14, 1967, 239) as a drynarioid fern, and transferred by them to *Astralopteris*.

Ecol. The species are all forest ferns; most of them grow in seasonally dry forest, others in everwet habitats. They mostly occur at low altitude, only a few species being sometimes found above 1500 m. The greater part of the species occur on rocks and especially in stream-beds, a naturally disturbed habitat. Some otherwise terrestrial species are sometimes also found as low-climbers (or as low-epiphytes). Some species are not rarely reported to form pure stands of many closely aggregated plants in forests (*B. sinensis*). Of *B. heteroclita* several forms occur which may cover (rocks of) stream-banks completely (HOLTTUM, Ferns Malaya, 1954, 463), one of these being an autotriploid.

Morph. The morphology, in particular of the Indian species, has been studied by NAYAR *c.s.* (for references see KAUR, J. Linn. Soc. Bot. 68, 1974, 153–162). In my monograph an elaborate treatment of the morphology and anatomy of all species is included to which the reader is referred for details.

The *rhizome* of some species bears ± conspicuous buds situated on the posterior side of the leaf-bases; they may develop into accessory branches. The stele is a dorsiventral dictyostele with wide overlapping leaf-gaps. The traces running into the buds or the accessory branch traces are situated at the posterior

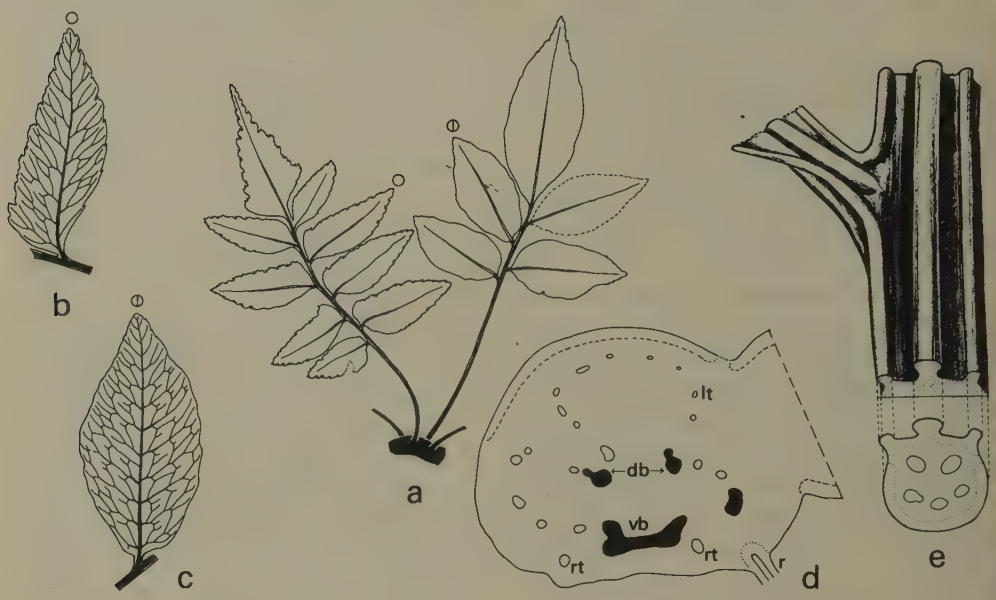

Fig. 25. *Bolbitis virens* (HOOK. & GREV.) SCHOTT. *a*. Juvenile plant, × 1/2, *b–c*. pinnae, nat. size. — *B. heteroclita* (PRESL) CHING. *d*. CS of rhizome, × 4; db = dorsal bundle, lt = leaf trace, r = root, rt = root trace, vb = ventral bundle. — *B. virens*. *e*. Adaxial view on junction of rachis with pinnae, and CS of lower part of rachis, × 7 (*a–c* HENNIPMAN 3320, *d* MANN *s.n.*, *e* HENNIPMAN 4047).

side of the two lateral leaf-gaps only, and are formed in association with root traces and leaf traces in an obviously characteristic arrangement.

Aerophores are part of the fronds but are continuous on the rhizome for some length. On the rhizomes of living material they show much variation in shape and size.

The *venation pattern* provides important characteristics for the discrimination of taxa. In all the species the secondary veins run parallel; typical differences are therefore expressed by the tertiary *etc.* veins only. See fig. 27, 31g, j, k. The venation in the pinnate fronds is anadromic.

Within the genus different types of venation occur. Veins are free in *ser. Egenolfianae*. In *ser. Heteroclitae* and *ser. Quoyanae* the pattern is sagenioid; the veins anastomosing in a reticulate pattern, with ± isodiametric or elongate, angulate areoles, and generally without recurrent included free veins. In *ser. Bolbitianae* the veins anastomose to form a costal areole and one to many smaller distal ones, the veins near the margin running ± parallel, the areoles with or without excurrent included free veins.

A so-called irregular venation, *i.e.* a venation in which the arrangements of the veins in the areas included by the secondary veins are markedly different, is often (not always!) present in alloploids, hybrids, and in crossings between cytotypes of one species.

The morphological evidence as given in my monograph indicates that divergent evolution in ferns with a sagenioid venation — the condition which I regard to represent the original condition in the genus — may lead to species having either a free venation or a venation with several types of included free, ex- and/or recurrent veins.

All species have *bulbils* subterminally (or terminally) on the sterile (and fertile) fronds. Bulbils are ± globular, persistent structures, situated adaxially; they are covered with scales similar to those on the rhizome. Development into mature plants occurs when the apex of the mother leaf strikes the ground; under humid conditions bulbils may develop into small plants on the erect lamina. Plants grown from bulbils stay connected with the mother plant for some time ('walking ferns').

The shape of the *fertile segments* is usually about the same (though much contracted) as that of the sterile ones. The margin of the segments often lack the prominent marginal projections found in the sterile material; bulbils are less prominent or even absent. Fronds that are in part fertile and in part sterile — so-called intermediate fronds — do not rarely occur and show much variation as to the sporangial arrangement, also in one species.

The venation pattern of the fertile segments is similar to that in the sterile ones; free included veins and small areoles are however less frequent or even absent. NAYAR *c.s.* (see KAUR, *l.c.*) reported a special kind of venation pattern occurring in the fertile fronds of the present genus; this is incorrect.

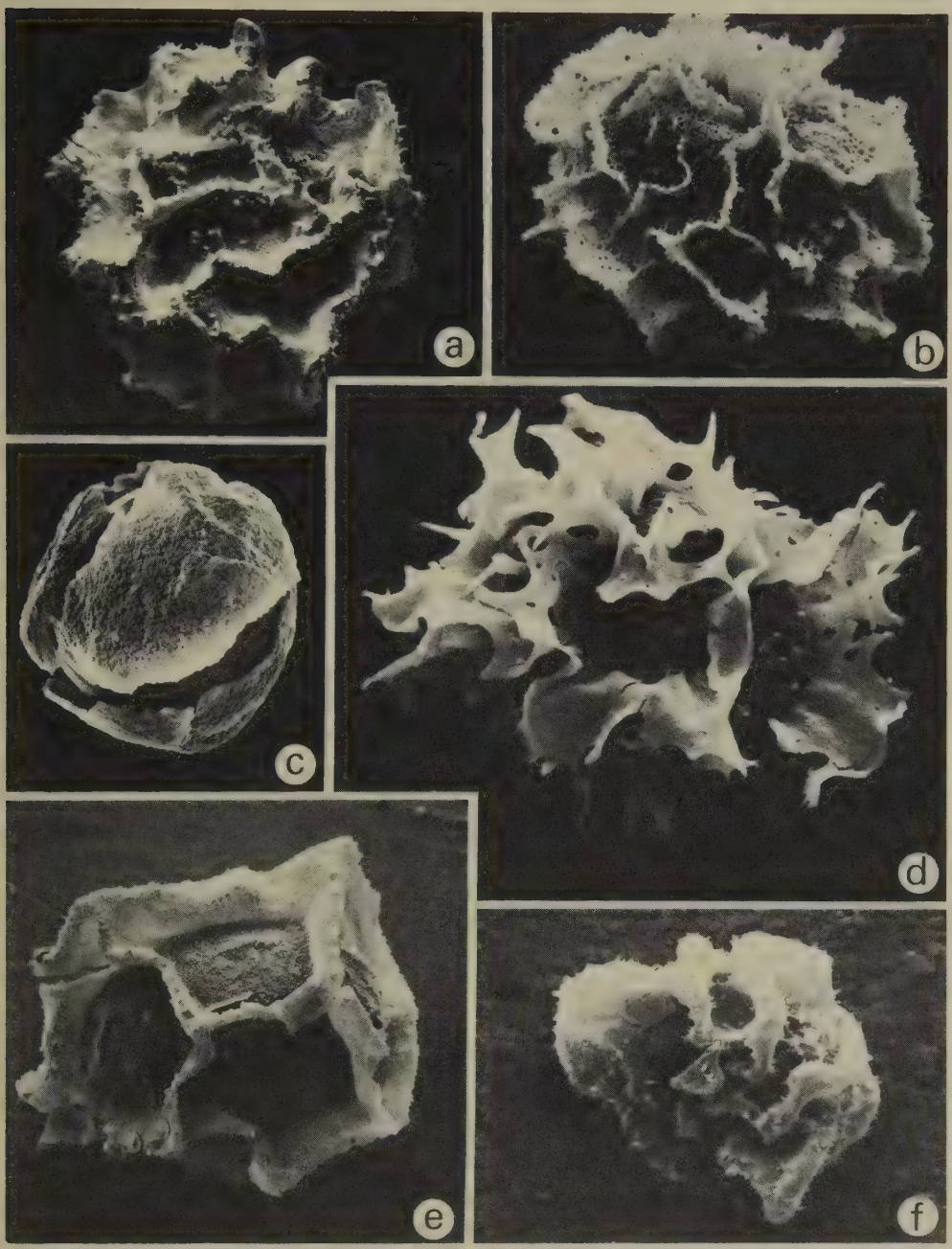

Fig. 26. Scanning electron micrographs of spores of Lomariopsidoid ferns. *a. Bolbitis sinensis*, × 1000 (HENNIPMAN 3229); *b. B. appendiculata ssp. appendiculata*, × 1000 (BUNAK 743); *c. B. angustipinna*, × 1000 (HENNIPMAN 3536); *d. Lomariopsis intermedia*, × 500 (BRASS 27982); *e. L. kingii*, × 750 (BRASS 32384); *f. Elaphoglossum callifolium*, × 1000 (LÖRZING 13523).

Insertion of the sporangia is variable; in some species the sporangia are situated all over the lower surface, in other species they are present on the veins only; also both conditions may be present in one species. Sporangia are formed in dense masses. In spite of the basipetal development of the fertile frond, sporangia of all parts of the frond reach maturity at the same time.

Spores as seen with the light microscope are monolete, biconvex, and provided with a variously shaped brown perispore. The exospore is thin, structurally not differentiated, and shows a short leasura. The perispore as seen from cross-sections studied with the electron microscope (HENNIPMAN, Acta Bot. Neerl. 19, 1970, 671–680) is composed of two more or less distinct elements, of which the outer perispore can also be recognized with the light microscope. Using properties of the (outer) perispore, three types of spores can be recognized with the light microscope. In *B. appendiculata* the perispore is reticulate and cristate. A smooth and undulate perispore is a characteristic of *ser. Bolbitianae*. All other species have a smooth, cristate-undulate or cristate perispore. Although some are characterized by either a cristate or a cristate-undulate perispore, the spores of several other species display both types of perispore as well as the intermediates.

Karyology. The haploid chromosome number of a considerable number of taxa as listed in my monograph was either 41 or 82. One species (*B. sinuata*) showed a weak indication of aneuploidy. In *ser. Bolbitianae* and *ser. Egenolfianae* only diploids were found. Of 20 specimens belonging to the 4 Malesian species of *ser. Heteroclitae* and *ser. Quoyanae*, 12 were diploids and 8 (auto)triploids; this obscured the delimitation of species of these two series in the past. Thus far apogamy has not been reported for the genus.

Gametophytes. Cordate(-elongate) and elongate gametophytes have been reported by NAYAR & KAUR (Bot. Rev. 37, 1971, 295–396), ATKINSON (in Jermy *c.s.* J. Linn. Soc. Bot., Suppl. 1, 1973, 81) and HENNIPMAN (*l.c.*). The gametophytes are either naked or may bear uniseriate glandular hairs or small glandular scales (the diploid prothallus of *B. repanda*).

Juvenile fronds. The ontogenetic frond stages of several species are surprisingly diverse. During ontogenesis features of the frond may become gradually or ± abruptly more complex when subsequent fronds on a single rhizome are compared. Abrupt changes were observed for instance in the shapes of the terminal segment and the pinnae, and the venation pattern (fig. 25a–c).

Also, comparable frond stages of different juvenile plants of one species may show variation. For instance in *B. virens* juvenile fronds were found with a triangular terminal segment (the less complex condition) and a rather intricate venation, as well as fronds showing a terminal pinna (the complex condition) but with a rather simple type of venation. This kind of variation — though often less clearly expressed — is also found in the adults. The variation in the morphology of the fronds of adult plants can to a certain extent be predicted when the morphology of the juvenile fronds is known.

Speciation. From the comparative study of the juvenile fronds it may be deduced that neotenous processes may have played an important role. Quite a number of dwarfs formerly given distinct status (*e.g. Edanyoa difformis*) could be referred to the *B. heteroclita* complex after it was found out that the mature fronds of these dwarfs were similar to both the ontogenetic frond stages of well-developed plants and the juvenile fronds grown from bulbils attached to such plants. The juvenile fronds grown from bulbils are generally more complex than the juvenile fronds of the same size grown from sporelings.

The mature fronds of *B. appendiculata ssp. appendiculata* (*ser. Egenolfianae*) are surprisingly similar to the juvenile fronds with free veins as found in several Asian species of *ser. Bolbitianae*. The idea that *B. appendiculata* arose by retention of certain juvenile characters from *ser. Bolbitianae* is supported by the occurrence of several hybrids between species belonging to the two series.

The recognition of *precocious fructification* in relation to the occurrence of morphologically different ontogenetic frond stages has been of great importance for the circumscription and phylogenetic considerations of the taxa.

Specific delimitation. Hybridisation between different species and between cytotypes of one species, auto- and alloploidisation is supposed to be a common phenomenon in the genus. Precocious fructification further adds to the surprising morphological variation found in several species(-aggregates).

Hybrids have aborted spores or aborted spore-mother-cells, and may multiply vegetatively (a property of all Malesian taxa).

Taxonomy. The genus *Bolbitis* was founded by SCHOTT (Gen. Fil. 1835, *ad t.* 13) for a part of *Acrostichum* with a creeping rhizome and anastomosing veins. At the same time (*l.c. ad t.* 16) he accommodated the Asian species with free veins in *Egenolfia*, keeping the American free-veined species separate in *Polybotrya*. PRESL (Tent. Pterid. 1836) and FÉE (Hist. Acrost. 1845) referred the species to several different genera whereas HOOKER (Spec. Fil. 5, 1864) and BAKER (in Hooker & Baker, Syn. Fil. 1865–1868) merged all acrostichoids again in *Acrostichum*. In spite of J. SMITH (Gen. Fil. 1875) who reinstated *Egenolfia*, CHRIST (Farnkräuter der Erde, 1897) and DIELS (in E. & P. Nat. Pfl. Fam. 1, 4, 1899) referred all the free-veined species again to *Polybotrya*, those with anastomosing veins to the heterogeneous *Gymnopteris*. CHRISTENSEN (Ind. Fil. 1906) recognized *Egenolfia*, including the other species in an assemblage he called *Leptochilus*. COPELAND (Philip. J. Sc. 37, 1928, 333–416) attempted to clear up the heterogeneities called *Gymnopteris* by DIELS and *Leptochilus* by CHRISTENSEN. He referred the Old World species to *Campium* in which he included a number of unrelated ferns as well. CHING (Bull. Fan Mem. Inst. Biol. 2, 1931, 297–317) monographed *Egenolfia*. He later (in Christensen, Ind. Fil. Suppl. 3, 1934) reinstated *Bolbitis* and largely delimited the genus as presented in my book. IWATSUKI (Acta Phytotax. Geobot. 18, 1959, 44–59) studied the Japanese species and was the first to unite *Egenolfia* and *Bolbitis*. The emended genus he divided into 4 sections. In my monograph most of the species are accommodated in 10 series (4 in Asia all except *ser. Bolbitianae* endemic), whereas several species of hybrid origin are separately ranked as *species incertae sedis*.

Notes. The treatment of the 12 recognized species is followed by the record of 5 hybrids and 2 dubious species. Of the latter two categories only those have been inserted in the key which were collected in more than one locality. Their numbers are preceded by **H** and **D** respectively.

The synonymy has been restricted to those names which were used for Malesian taxa. No types are cited because they seem not useful for botanists consulting this Flora. For full synonymy and types see my monograph.

So-called intermediate fronds, dwarfs and aberrant specimens are generally not considered in the descriptions.

The term segment is used for a portion of the lamina that has an axis and is not a pinna. Of the (central) segments the index (length/width ratio) is generally given.

The number of pinnae given refers to the total number of pinnae to a frond.

Caudate apices of pinnae are not included in the measures given for the length of the pinnae.

Primordia of bulbils can be traced when the sterile fronds are examined in transmitted light. They appear as small knobs terminally or subterminally.

The costa of the pinna and the simple lamina are termed the primary vein; the pinnately arranged lateral veins are designated as the secondary veins.

Chromosome numbers given are taken from the list supplied in my monograph.

The key to the species is based on characters of the sterile fronds, and sometimes on those of the spores. Identification will be possible for most of the material using a good hand lens and preferably also a source of transmitted light to study the venation pattern.

KEY TO THE SPECIES AND HYBRIDS[1]

1. Plants small (dwarfed) and/or fronds simple.
 2. Bulbil ± terminal. Pinnae 16–30 . . . . . **11. B. novoguineensis**
 2. Bulbils subterminal (or absent). Pinnae less.
  3. Veins irregularly anastomosing, usually with many ex- and recurrent free veins. Fronds entire or (bi)trifid . . . . . **H.5. Leptochilus × trifidus**
  3. Veins regularly anastomosing, without free veins or with few ex- and recurrent free veins. Fronds entire.
   4. Fronds coriaceous.
    5. Areoles (except the costal one) all of about the same shape, decreasing in size towards the margin **10. B. rivularis**
    5. Areoles of different size and shape, not decreasing in size towards the margin . . **8. B. sinuata**
   4. Fronds herbaceous (to subcoriaceous).
    6. Fronds pinnate. Venation of terminal segment as in fig. 31j, k . . . . . **9. B. quoyana**
    6. Fronds entire or if pinnate with a venation as in fig. 31g or simpler . . . . **7. B. heteroclita**
1. Plants not dwarfed. Fronds pinnate.
 7. Veins free.
  8. Bulbil ± terminal on the lamina. Spines on the margin of the pinnae ± flattened at their bases. Base of pinnae symmetrical . . . . . **5. B. rhizophylla**
  8. Bulbil subterminal on the lamina. Spines on the margin not flattened at their bases. Base of pinnae symmetrical or asymmetrical.
   9. Perispore smooth. Base of pinnae symmetrical, margin lobed $^1/_3$–$^2/_3$(–$^3/_4$) towards the costa **6. B. sinensis**
   9. Perispore reticulate. Base of pinnae either symmetrical or asymmetrical; if symmetrical, margin of the pinnae entire or lobed to $^1/_3$(–$^1/_2$) towards the costa . . . . . **4. B. appendiculata**
 7. Veins anastomosing.
  10. Fronds ± coriaceous.
   11. Terminal segment conform to the pinnae, though usually larger . . . . . **8. B. sinuata**
   11. Terminal segment triangular . . . . . **10. B. rivularis**
  10. Fronds herbaceous.
   12. Fronds drying reddish. Perispore undulate . . . . . **2. B. scalpturata**
   12. Fronds drying greenish. Perispore undulate, cristate-undulate, or cristate.
    13. Terminal segment conform to the pinnae or composed of 2 or 3 lobes.
     14. Venation pattern with many excurrent included free veins.
      15. Perispore undulate . . . . . **3. B. virens *var.* compacta**
      15. Perispore cristate . . . . . **D.1. B. interlineata**
     14. Venation pattern without or with only few excurrent (and recurrent) included free veins.
      16. Pinnae 2–10(–15) to a frond . . . . . **7. B. heteroclita**
      16. Pinnae more than 15 to a leaf . . . . . **1. B. angustipinna**
    13. Terminal segment triangular.
     17. Bulbil ± terminal. Small plant . . . . . **11. B. novoguineensis**
     17. Bulbil subterminal.
      18. Terminal segment narrowly triangular. Perispore undulate . . . . . **1. B. angustipinna**
      18. Terminal segment triangular. Perispore cristate or cristate-undulate.

(1) Only hybrids known from more than one locality are included.

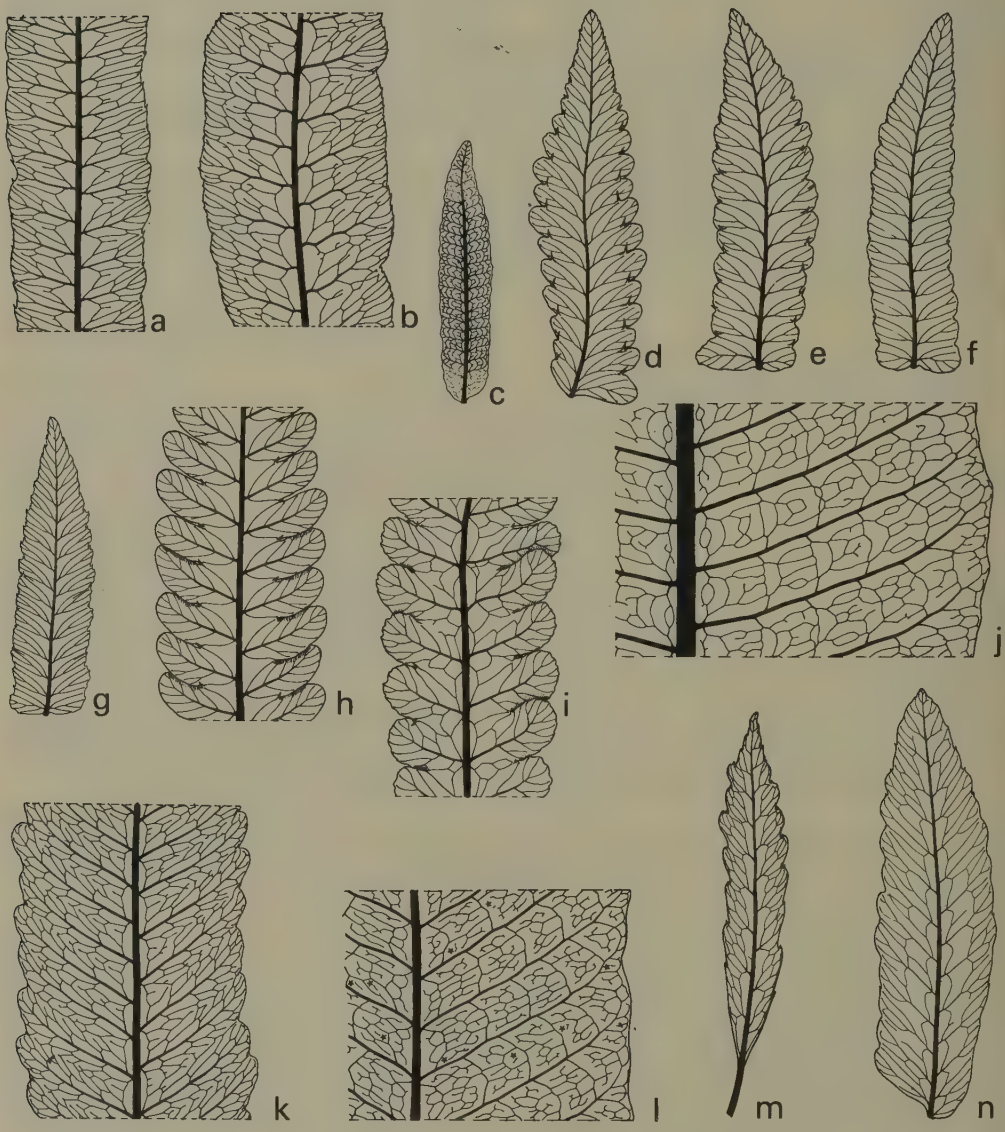

Fig. 27. Venation patterns of sterile (*a–b*, *d–n*) and fertile (*c*) pinnae, × 4/5. *a. Bolbitis angustipinna* (HENNIPMAN 3637), *b. B. scalpturata* (MOUSSET 562), *c. B. virens var. compacta* (SF 29084), *d. B. appendiculata ssp. appendiculata* (HOLTTUM *s.n.*, SING); *e–f. B. appendiculata ssp. vivipara var. neglecta* (VAN BORSSUM WAALKES 603); *g. B. rhizophylla* (LEROY TOPPING 655); *h. B. sinensis* (HENNIPMAN 3229A); *i. B. repanda* (SF 25585); *j. B. sinuata* (JOHNSON *s.n.*, L); *k. B. interlineata* (BROOKS 12); *l. Leptochilus* × *trifidus* (VAN ALDERWERELT VAN ROSENBURGH *s.n.*, L); *m. B.* × *sinuosa nm. foxii* (PNH 8904); *n. B.* × *singaporensis* (HOLTTUM *s.n.*, SING).

19. Venation pattern irregular. See fig. 27i . . . . . **12. B. repanda**
19. Venation pattern regular.
20. Base of pinnae narrow-acute or -cuneate. Pinnae $7^1/_2$–12 by 1–$1^3/_4$ cm **H.4. B. × sinuosa**
20. Base of pinnae wider. Pinnae usually larger . . . . . **9. B. quoyana**

1. Series Bolbitianae

HENNIPMAN, Leid. Bot. Ser. 2 (1977) 147. — *Bolbitis* SCHOTT, Gen. Fil. (1835) *ad t.* 13, *typo incl., pro genere.*

Sterile fronds pinnate; lamina with a (primordium of a) subterminal bulbil; pinnae 3–50, the margin sometimes with inconspicuous spines in the sinuses; terminal segment usually conform to the pinnae, sometimes narrowly triangular; venation pattern: veins variously anastomosing, always with a costal areole, with or without excurrent included free veins. Spores with a smooth, undulate perispore. — Chromosomes n = 41, 2n = (*c.*) 82.

Distr. Pantropical; most diversified in Asia (7 *spp.*, of which 3 in *Malesia*).

Note. A very homogeneous series. *B. angustipinna*, the most widespread Asian representative, is most closely related to the species from America and Africa.

1. Bolbitis angustipinna (HAYATA) ITO, J. Jap. Bot. 14 (1938) 443; HENNIPMAN, Leid. Bot. Ser. 2 (1977) 152, f. 40a–f. — *Leptochilus angustipinnus* HAYATA, Ic. Pl. Form. 5 (1915) 297, f. 119. — *Campium angustipinnum* COPEL. Philip. J. Sc. 37 (1928) 381, f. 33.

Leptochilus cuspidatus (PRESL) C.CHR. *var. crenatus* ROSENST. Hedwigia 56 (1915) 348.

[*Acrostichum contaminans* WALL. Cat. (1829) *n.* 22, *nomen.* — *Poecilopteris contaminans* MOORE, Ind. Fil. (1857) 8, *nomen.*] — *Acrostichum crispatulum* CLARKE *var. contaminans* CLARKE, Trans. Linn. Soc. Bot. 1 (1880) 580, pl. 84: f. 2A, 2C. — *B. contaminans* CHING in C.Chr. Ind. Fil. Suppl. 3 (1934) 47; IWATSUKI, Acta Phytotax. Geobot. 18 (1959) 53, f. 9; DEVOL & KUO, Fl. Taiwan 1 (1975) 348. — **Fig. 26c, 27a.**

Sterile fronds pinnate, 55–150 cm long; lamina index 1–3, 30–90 by 20–45 cm, terminal segment 8–25 cm long, (firm) herbaceous, usually light to dark green, sometimes with a purple tinge; pinnae 20–50, index 5–12, the central part usually with parallel margins, 11–30 by 2–3(–5) cm, base ± symmetrical, acute, broadly attenuate or truncate, margin usually slightly serrate-crenate, sometimes lobed to $^1/_3$ to the costa and with a short or inconspicuous spine in each sinus; *terminal segment* usually narrowly triangular, sometimes ± conform to the central pinnae; *venation pattern:* veins forming a costal areole and one to several rows of distal areoles, included free veins absent, the veins in the marginal strip excurrent and parallel; see fig. 27a. *Fertile fronds* 55–160 cm long; pinnae index (6–)9–20, 5–23 by 0.4–1.7 cm. *Sporangia* situated usually all over the lower surface, sometimes with a sterile strip along the costa. Spores smooth, undulate.

Distr. Ceylon, Himalayas eastwards to S. China and Taiwan, southwards to N. Thailand; in *Malesia:* Philippines (Luzon), one collection.

Ecol. On rocks in monsoon and evergreen forest, 250–1500 m.

2. Bolbitis scalpturata (FÉE) CHING in C.Chr. Ind. Fil. Suppl. 3 (1934) 50; BACKER & POSTH. Varenfl. Java (1939) 82, *p.p.*; POSTH. Ann. Bot. Gard. Btzg vol. hors série (1944) 62; HENNIPMAN, Leid. Bot. Ser. 2 (1977) 163, f. 43a–d. — *Heteroneuron scalpturatum* FÉE, Hist. Acrost. (1845) 95, pl. 56, *p.p.* — *Leptochilus scalpturatus* C.CHR. Ind. Fil. (1906) 387, *p.p.*; V.A.V.R. Handb. Mal. Ferns (1908) 743, *p.p.* — *Campium scalpturatum* COPEL. Philip. J. Sc. 37 (1928) 383, f. 35; BACKER & POSTH. Nat. Tijd. N. I. 93 (1933) 162.

Leptochilus reimersii RENSCH, Hedwigia 74 (1934) 249, pl. 7: f. 2. — **Fig. 27b.**

Sterile fronds pinnate, 25–90 cm long; lamina index 1–3, 20–55 by 7–30 cm, terminal segment 9–20 cm long, herbaceous to subcoriaceous, purplish or purplish-brown; pinnae 4–24, index 3–7, 5.5–17.5 by 1.5–4 cm, base ± symmetrical, narrowly to broadly cuneate, margin ± entire or finely serrate-crenate, without spines, apex acute to (long-)acuminate; *terminal segment* usually conform to the central pinnae, sometimes narrowly triangular and/or somewhat prolonged; *venation pattern:* veins forming a network of a costal areole and one to few transverse rows of smaller distal ones, part of the areoles with few to several, mostly excurrent included free veins; see fig. 27b. *Fertile fronds* 30–70 cm long; pinnae index 3–8, 3–9 by 0.6–1.5 cm. *Sporangia* inserted mostly on and near the veins, either all over the lower surface, arranged acrostichoid, or along the margin only, arranged pteridoid. Spores smooth, undulate.

Distr. E. Burma to Indo-China; in *Malesia:* S. Sumatra (Lampongs), E. Java (Mt Tengger), Lesser Sunda Is. (Bali, Sumbawa, Flores), S. Celebes (also Saleyer Is.), Philippines (Palawan, Luzon).

Ecol. Showing a preference for a seasonal climate, 0–1200 m.

Note. A somewhat critical species. The venation pattern shows considerable variation; it may come near to that of *B. angustipinna* or *B. virens.*

3. Bolbitis virens (HOOK. & GREV.) SCHOTT, Gen. Fil. (1835) *ad t.* 13; HOLTTUM, Ferns Malaya (1954) 468, f. 275, *p.p.* — *Campium virens* PRESL, Tent. Pterid. (1836) 239; COPEL. Philip. J. Sc. 37 (1928) 388; HENNIPMAN, Leid. Bot. Ser. 2 (1977) 180, f. 47 & 48. — *Leptochilus virens* C.CHR. Ind. Fil. (1906) 388, *p.p.*; V.A.V.R. Handb. Mal. Ferns (1908) 741, *p.p.*; *ibid.* Suppl. (1917) 435, *p.p.*

var. **compacta** HENNIPMAN, Blumea 18 (1970) 149; Leid. Bot. Ser. 2 (1977) 184, f. 48i, j. — **Fig. 25a–c, e, 27c.**

Sterile fronds pinnate, 40–115 cm long; lamina index 1–3, 20–75 by 15–50 cm, terminal segment 14–40 cm long, firm herbaceous; pinnae 6–22, index 3–7, 10–30 by 2.5–6.5 cm, base ± symmetrical, usually narrowly, sometimes broadly attenuate or cuneate, margin usually ± entire, sometimes (bi)serrate or (bi)serrate-crenate; *terminal segment* conform to the pinnae or somewhat prolonged; *venation pattern:* veins forming a costal

areole and several to many equally large distal ones, the arches with two or more excurrent free veins. *Fertile fronds* 40–125 cm long; central pinnae index 3–8, 4–11.5 by 0.8–2 cm. *Sporangia* inserted all over the lower surface. Spores smooth, undulate.

Distr. ?India (Nicobar Is.), S. Vietnam, Peninsular Thailand; in *Malesia:* Malay Peninsula (Kedah, Selangor, Penang, Langkawi Is.). Fig. 28.

Ecol. Usually on rocks and often near streams in (dry) evergreen forest, 0–400(–700) m.

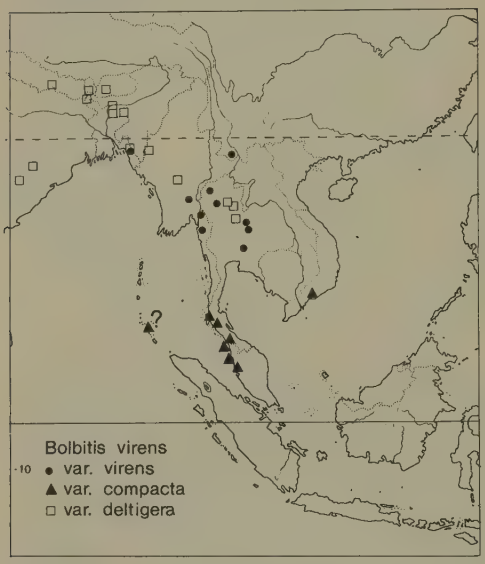

Fig. 28. Range of *Bolbitis virens* (HOOK. & GREV.) SCHOTT.

2. Series Egenolfianae

HENNIPMAN, Leid. Bot. Ser. 2 (1977) 185. — *Egenolfia* SCHOTT, Gen. Fil. (1835 or 1836) *ad t.* 16, *typo incl., pro genere.*

Sterile fronds pinnate; lamina with one, usually subterminal, in one species (*B. rhizophylla*) ± terminal bulbil; pinnae 14–90, the margin with spines corresponding to the most distal acroscopic tertiary vein of each secondary vein; terminal segment triangular; venation: veins free. Spores with either a smooth, cristate or cristate-undulate perispore, or with a reticulate ± cristate perispore. — Chromosomes n = 41, 2n = 82.

Distr. S. India and Ceylon to *W. Malesia*, northwards to S. Japan.

4. Bolbitis appendiculata (WILLD.) IWATSUKI, Acta Phytotax. Geobot. 18 (1959) 48; HENNIPMAN, Blumea 18 (1970) 147; Leid. Bot. Ser. 2 (1977) 185, f. 49. — *Acrostichum appendiculatum* WILLD. Sp. Pl. 5 (1810) 114; HOOK. Exot. Fl. 2 (1825) 108, pl. 108; Sp. Fil. 5 (1864) 251, *p.p.*; BAKER in Hook. & Baker, Syn. Fil. (1868) 415. — *Polybotrya appendiculata* J. SMITH, Hook. J. Bot. 4 (1841) 150; v.A.v.R. Handb. Mal. Ferns (1908) 724, *p.p.* — *Egenolfia appendiculata* J. SMITH, Ferns Br. For. (1866) 111, fig.; BACKER & POSTH. Nat. Tijd. N. I. 93 (1933) 153; Varenfl. Java (1939) 84, f. 14; HOLTTUM, Ferns Malaya (1954) 459, f. 270; COPEL. Fern Fl. Philip. (1960) 266; DEVOL & KUO, Fl. Taiwan 1 (1975) 350, pl. 123.

Polybotrya vivipara HAM. *ex* HOOK. Exot. Fl. 2 (1825) 107, pl. 107. — *Egenolfia vivipara* C.CHR. Ind. Fil. Suppl. 3 (1934) 102. — *B. hookeriana* IWATSUKI, Acta Phytotax. Geobot. 18 (1959) 49. — *B. appendiculata* (WILLD.) IWATSUKI *ssp. vivipara* HENNIPMAN, Blumea 18 (1970) 147; Leid. Bot. Ser. 2 (1977) 195, f. 50, 51.

Polybotrya marginata BL. En. Pl. Jav. (1828) 100, *nom. superfl.*; Fl. Java Filices (1829) 18, pl. 3; FÉE, Hist. Acrost. (1845) 75. — *Polybotrya appendiculata* (WILLD.) J. SMITH *var. marginata* C.CHR. Bot. Tidsskr. 32 (1916) 343.

[*Acrostichum hamiltonianum* WALL. Cat. (1829) *n.* 28, *nomen.*] — *Polybotrya hamiltoniana* [PRESL, Tent. Pterid. (1836) 236, *nomen*;] FÉE, Hist. Acrost. (1845) 78, *nom. superfl.* — *Egenolfia hamiltoniana* FÉE, Genres Polyp. (1852) 48, *non* SCHOTT, 1835 or 1836 (= *B. appendiculata ssp. appendiculata*). — *Acrostichum appendiculatum* WILLD. *var. hamiltonianum* BAKER in Hook. & Baker, Syn. Fil. (1868) 415. — *Polybotrya appendiculata* (WILLD.)

Fig. 29. Range of *Bolbitis appendiculata* (WILLD.) IWATSUKI.

J. SMITH *var. hamiltoniana* BEDD. Handb. Ferns Br. India (1883) 426, f. 256, *p.p.*; v.A.v.R. Handb. Mal. Ferns (1908) 724, *quoad nomen solum*; *ibid.* Suppl. (1917) 431, *ditto*.

B. appendiculata (WILLD.) IWATSUKI *var. neglecta* HENNIPMAN, Blumea 18 (1970) 147; Leid. Bot. Ser. 2 (1977) 197, f. 50i–n, 51. — **Fig. 26b, 27d–f.**

Sterile fronds pinnate, 15–100 cm long; lamina index 2–6(–8), 10–80 by 2.5–20 cm, terminal segment 1–10 cm long, herbaceous, usually olivaceous; pinnae (20–)25–60(–85), index 2–5(–7), 1.5–10(–15) by 0.5–2.5 cm, base symmetrical to strongly oblique, margin ± entire, finely serrate, or lobed to $^1/_3$ ($^1/_2$) towards the costa; *terminal segment* triangular, apex sometimes somewhat prolonged; *venation pattern:* secondary veins on either side with 2 or 3 tertiary veins; see fig. 27d–f. *Fertile fronds* 15–90 cm long; pinnae index 1–6, 0.2–11 by 0.15–1.7 cm. *Sporangia* inserted all over the lower surface or ± restricted to the veins. Spores with a reticulate cristate perispore. — Chromosomes n = 41, 2n = 82.

Distr. S. India and Ceylon, NE. India eastwards through SE.–E. continental Asia to S. Japan; in *Malesia:* Malaya, Java, Philippines. Fig. 29.

Ecol. On rocks or in soil in deciduous and evergreen forest, 0–1500 m.

Note. The reticulate perispore is unique in the genus.

KEY TO INFRASPECIFIC TAXA

1. Fertile pinnae with a lamina. Sporangia situated on the lower surface of the frond **a.** *ssp.* **appendiculata**
1. Fertile pinnae with a narrow strip of lamina present along the costa only. Sporangia facing to all directions **b.** *ssp.* **vivipara** *var.* **neglecta**

a. *ssp.* **appendiculata** — *Acrostichum appendiculatum* WILLD. — *Polybotrya marginata* BL. — **Fig. 27d.**

Sterile fronds 15–60(–80) cm long, the rachis with a narrow wing; pinna base oblique. Fertile fronds: pinna index 1–6, 0.25–4 by 0.2–0.7 cm. Sporangia inserted mainly on the veins or all over the lower surface.

Distr. Ceylon, S. India, Himalayas eastwards to S. Japan and Indo-China; in *Malesia:* Sumatra (West Coast, Bencoolen, East Coast), Malay Peninsula, Java (West, Central). Fig. 29.

Ecol. See the species.

b. *ssp.* **vivipara** (HOOK.) HENNIPMAN, Leid. Bot. Ser. 2 (1977) 195. — *Polybotrya vivipara* HAM. *ex* HOOK.. — *B. appendiculata* (WILLD.) IWATSUKI *var. neglecta* HENNIPMAN.

var. **neglecta** HENNIPMAN, Blumea 18 (1970) 147; Leid. Bot. Ser. 2 (1977) 197, f. 50i–n, 51.

Polybotrya appendiculata (WILLD.) J. SMITH *var. rhizophylla auct. non* (KAULF.) KUHN: KUHN, Ann. Mus. Bot. Lugd.-Bat. 4 (1869) 225.

Polybotrya appendiculata (WILLD.) J. SMITH *var. hamiltoniana auct. non* (FÉE) BEDD.: v.A.v.R. Handb. Mal. Ferns, Suppl. (1917) 431. — **Fig. 27e, f.**

Sterile fronds 30–50 cm long, the rachis with a narrow or inconspicuous wing; pinna base ± symmetrical or oblique. Fertile fronds: pinnae ± moniliform, index 5–15, 0.7–3 cm long, with a narrow strip of lamina along the costa. Sporangia mainly inserted at the endings of the lateral veins.

Distr. India (Andaman and Nicobar Is.); in *Malesia:* West Java. Fig. 29.

Ecol. On stone, 70 m (type).

5. Bolbitis rhizophylla (KAULF.) HENNIPMAN, Blumea 18 (1970) 148; Leid. Bot. Ser. 2 (1977) 199, f. 52d–r, 53. — *Gymnogramma rhizophylla* KAULF. En. Fil. (1824) 78. — *Polybotrya rhizophylla* PRESL, Tent. Pterid. (1836) 231; FÉE, Hist. Acrost. (1845) 77; METT. Fil. Hort. Lips. (1856) 24. — *Egenolfia rhizophylla* FÉE, Genres Polyp. (1852) 48; COPEL. Fern Fl. Philip. (1960) 266; DEVOL & KUO, Fl. Taiwan 1 (1975) 352.

Polybotrya intermedia [J. SMITH, HOOK. J. Bot. 3 (1841) 72, *nomen*;] FÉE, Hist. Acrost. (1845) 76, pl. 40: f. 1. — *Egenolfia intermedia* FÉE, Genres Polyp. (1852) 48; CHING, Bull. Fan Mem. Inst. Biol. 2 (1931) 308; COPEL. Fern Fl. Philip. (1960) 266. — *B. intermedia* IWATSUKI, Acta Phytotax. Geobot. 18 (1959) 49.

Polybotrya neglecta FÉE, Hist. Acrost. (1845) 76, pl. 39: f. ii.

Polybotrya serrulata [J. SMITH, Hook. J. Bot. 3 (1841) 401, *nomen*;] FÉE, Hist. Acrost. (1845) 76, pl. 39: f. ii*. — *Egenolfia serrulata* FÉE, Genres Polyp. (1852) 358. — *B. serrulata* IWATSUKI, Acta Phytotax. Geobot. 18 (1959) 49.

Polybotrya exaltata BRACKENR. in Wilkes, U.S. Expl. Exp. 16 (1854) 78.

Polybotrya duplicato-serrata HAYATA, Ic. Pl. Form. (1915) 305, f. 123A.

Egenolfia fluviatilis COPEL. Philip. J. Sc. 38 (1929) 152, pl. 5; Fern Fl. Philip. (1960) 267. — *B. copelandii* IWATSUKI, Acta Phytotax. Geobot. 18 (1959) 49, *nom. illeg.*, *non* CHING *ex* TARDIEU-BLOT & C.CHR. 1938. — **Fig. 27g.**

Sterile fronds pinnate, 20–90 cm long; lamina index 3–9, 18–80 by 4.5–15 cm, terminal segment 1–6 cm long, herbaceous, green to blackish, the petiole and lower side of the basal part of the rachis usually with small, blackish, spreading, ± permanent scales; rachis with a narrow wing except for the lowest part; pinnae 35–90, up to 35 mm apart, index 2–6, 2.5–8 by 0.8–2 cm, base usually symmetrical, (narrowly) cuneate to subcordate, margin

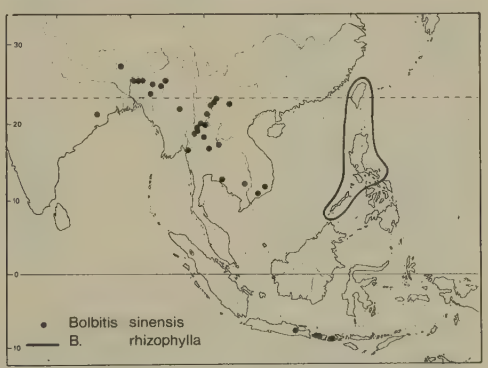

Fig. 30. Range of *Bolbitis sinensis* (BAKER) IWATSUKI and *B. rhizophylla* (KAULF.) HENNIPMAN.

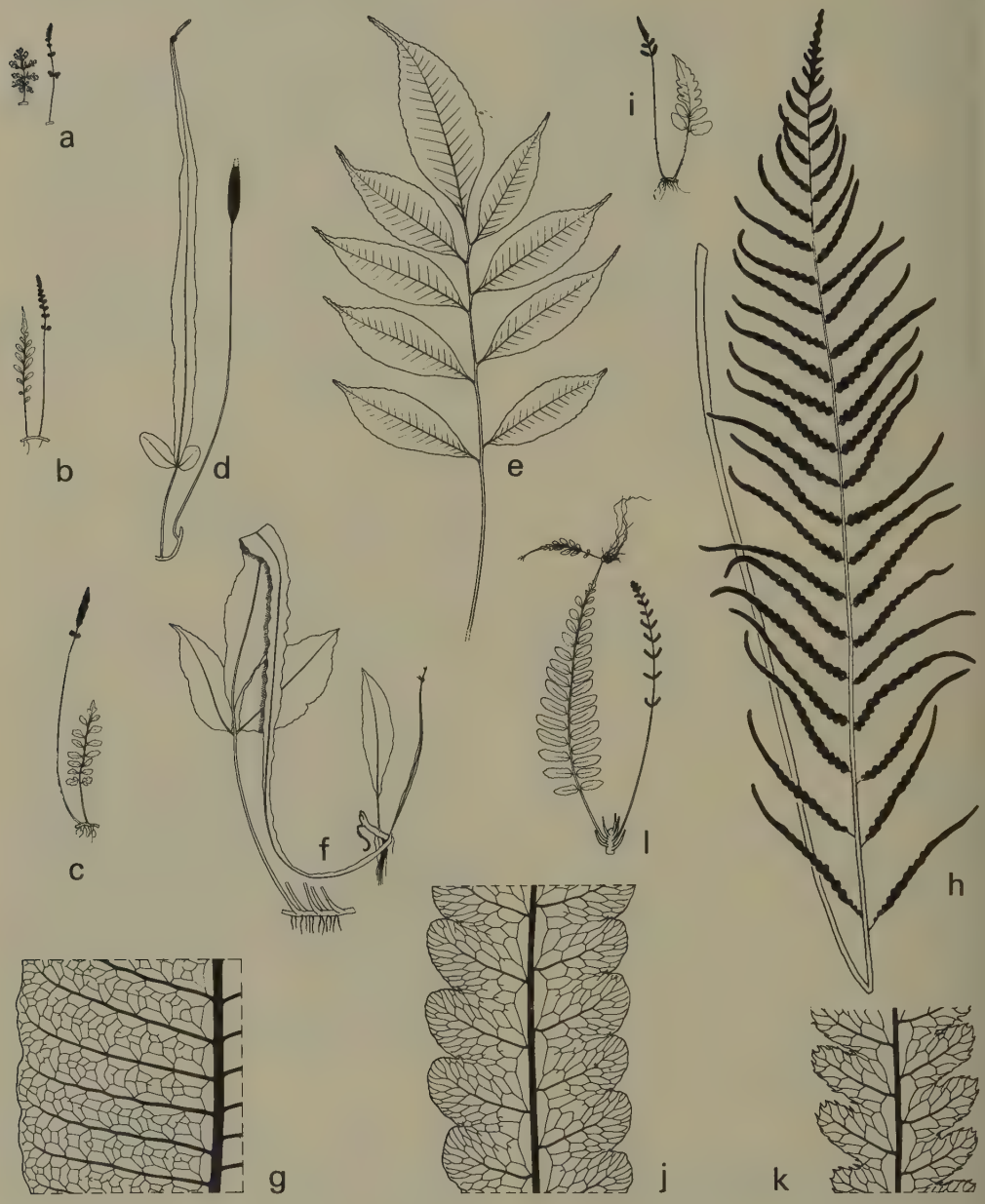

Fig. 31. *Bolbitis heteroclita* (PRESL) CHING. *a–f*. Habits, × 1/5, *g*. venation pattern of sterile pinna, × 4/5. — *B. quoyana* (GAUDICH.) CHING. *h–i*. Habits, × 1/5, *j–k*. venation patterns of sterile pinnae, × 4/5. — *B. novo-guineensis* HENNIPMAN. *l*. Habit, × 1/5 (*a* PRICE 2518A, *b* PRICE 351, *c* BS 28843, *d* PNH 8811, *e* JACOBS 7950, *f* HENNIPMAN 4069, *g* HENNIPMAN 3836, *h* WALKER T 10052, *i* SCHLECHTER 16163, *j* WALKER T 9604, *k* ELMER 13468a, *l* BRASS 28008).

finely serrate, biserrate, or serrately lobed to $^1/_3$ towards the costa, the spines often tooth-like; *terminal segment* narrowly triangular; venation pattern: *secondary veins* on either side with 1–3 tertiary veins, see fig. 27g. *Fertile fronds* 20–80 cm long; pinnae index 1–6, 0.4–3(–4) by 0.3–0.7 cm. *Sporangia* inserted on and near the veins. Spores with a smooth cristate-undulate perispore. — Chromosomes n = 41.

Distr. Taiwan; in *Malesia:* Philippines (Balabac I., Palawan, Mindoro, common in Luzon). Fig. 30.

Ecol. On rocks in moist forests and often near riverbanks, 0–1000 m.

6. Bolbitis sinensis (BAKER) IWATSUKI, Acta Phytotax. Geobot. 18 (1959) 49; HENNIPMAN, Leid. Bot. Ser. 2 (1977) 202, f. 53, 54. — *Acrostichum sinense* BAKER, Kew Bull. (1906) 14. — *Egenolfia sinensis* MAXON, Proc. Biol. Soc. Wash. 36 (1923) 173. — *Campium sinense* C.CHR. Contr. U.S. Nat. Herb. 26 (1931) 292.

Acrostichum appendiculatum WILLD. *var. costulatum* HOOK. Sp. Fil. 5 (1864) 252. — *Polybotrya appendiculata* (WILLD.) J. SMITH *var. costulata* BEDD. Ferns Br. India (1865) 110, pl. 110. — *Egenolfia bipinnatifida* J. SMITH, Hist. Fil. (1875) 132; BACKER & POSTH. Varenfl. Java (1939) 85. — *B. sinensis* (BAKER) IWATSUKI *var. costulata* TAGAWA & IWATSUKI, Acta Phytotax. Geobot. 22 (1967) 102. — **Fig. 27h.**

Sterile fronds pinnate, 35–145 cm long; lamina index 1–4(–5), 20–115 by 10–35 cm, terminal segments 8–35 cm long, herbaceous, dark green, ± glabrescent; rachis usually with a narrow wing except for the lowest part; pinnae 14–40, index 3–7, 5.5–17.5(–21) by 1.5–5 cm, base ± symmetrical, broadly cuneate to auricled, margin lobed $^1/_3$–$^2/_3$(–$^3/_4$) towards the costa, lobes spaced to partly overlapping, *c.* 6–8 mm wide at the base; *terminal segment* narrowly triangular, the apex usually either prolonged or flagelloid; *venation pattern:* secondary veins on either side with 4–6 tertiary veins, see fig. 27h. *Fertile fronds* 18–85 cm long; pinnae index 2–8, 1.3–6 by 0.4–1.2 cm. *Sporangia* usually mainly inserted on and near the veins. Spores with a smooth cristate-undulate perispore. — Chromosomes n = 41, 2n = 82.

Distr. S. China, E. Himalayas to Indo-China; in *Malesia:* E. Java (once), Lesser Sunda Is. (Bali, Sumbawa). Fig. 30.

Ecol. Usually terrestrial, creeping in soil or on rocks, sometimes low-epiphytic (up to 1 m), in (hill) evergreen (monsoon) forest, obviously a rare plant, 0–1900 m.

3. Series Heteroclitae

HENNIPMAN, Leid. Bot. Ser. 2 (1977) 220.

Sterile fronds simple or pinnate; petiole with 3–14 vascular bundles; lamina with usually one subterminal bulbil; pinnae 2–11(–15), the margin without teeth or spines; terminal segment usually conform to the pinnae, sometimes (in dwarfs) triangular; venation pattern: veins usually completely anastomosing into a regular network, areoles varying in size and shape. Spores with a smooth, cristate or cristate-undulate perispore. — Chromosomes n = 41, 2n = 82, *c.* 123.

Distr. NE. India to the Pacific, northwards to S. Japan; throughout *Malesia*, except for the Lesser Sunda Is.

7. Bolbitis heteroclita (PRESL) CHING in C.Chr. Ind. Fil. Suppl. 3 (1934) 48; BACKER & POSTH. Varenfl. Java (1939) 83, f. 13; HOLTTUM, Ferns Malaya (1954) 462, f. 271; COPEL. Fern Fl. Philip. (1960) 257; CHING, Fl. Hain. (1964) 165, f. 75; DEVOL & KUO, Fl. Taiwan 1 (1975) 348, pl. 122; HENNIPMAN, Leid. Bot. Ser. 2 (1977) 221, f. 60. — *Acrostichum heteroclitum* PRESL, Rel. Haenk. (1825) 15, pl. 2: f. 2. — *Heteroneuron heteroclitum* FÉE, Hist. Acrost. (1845) 92. — *Chrysodium heteroclitum* KUHN, Ann. Mus. Bot. Lugd.-Bat. 4 (1869) 294. — *Leptochilus heteroclitus* C.CHR. Ind. Fil. (1906) 385; v.A.v.R. Handb. Mal. Ferns (1908) 739. — *Campium heteroclitum* COPEL. Philip. J. Sc. 37 (1928) 359, f. 13; BACKER & POSTH. Nat. Tijd. N. I. 93 (1933) 163.

Nephrodium cuspidatum PRESL, Rel. Haenk. (1825) 31. — *Polystichum cuspidatum* PRESL, Tent. Pterid. (1836) 82. — *Heteroneuron cuspidatum* PRESL, Epim. Bot. (1851) 169. — *Chrysodium cuspidatum* KUHN, Ann. Mus. Bot. Lugd.-Bat. 4 (1869) 293, *p.p.* — *Leptochilus cuspidatus* C.CHR. Ind. Fil. (1906) 384, *quoad nomen solum.* — *Campium cuspidatum* COPEL. Philip. J. Sc. 37 (1928) 365, f. 19. — *B. cuspidata* CHING in C.Chr. Ind. Fil. Suppl. 3 (1934) 48; COPEL. Fern Fl. Philip. (1960) 259.

Acrostichum flagelliferum WALL. *ex* HOOK. & GREV. Ic. Fil. (1827) pl. 23, *p.p.*; BL. En. Pl. Jav. (1828) 104; Fl. Java Fil. (1829) 37, pl. 13, *p.p.* — *B. flagellifera* SCHOTT, Gen. Fil. (1835) *ad t.* 13. — *Gymnopteris flagellifera* BEDD. Ferns Br. India, Suppl. (1876) 27; COPEL. Polyp. Philip. (1905) 42, *p.p.*

Acrostichum proliferum BL. En. Pl. Jav. (1828) 104, *non* HOOK. 1844 (= *B. subcrenata*).

Leptochilus linnaeanus FÉE, Hist. Acrost. (1845) 87, pl. 47: f. 2, *excl. syn.*; v.A.v.R. Handb. Mal. Ferns (1908) 735; Suppl. Corr. (1917) 60. — *Dendroglossa linnaeana* FÉE, Gen. Polyp. (1852) 81. — *Gymnopteris linnaeana* CHRIST, J. de Bot. 19 (1905) 125; COPEL. Polyp. Philip. (1905) 4. — *Leptochilus heteroclitus* (PRESL) C.CHR. *var. linnaeanus* CHRIST, Philip. J. Sc. 2 (1907) Bot. 160. — *Campium linnaeanum* COPEL. Philip. J. Sc. 37 (1928) 343, *quoad nomen solum*; BACKER & POSTH. Nat. Tijd. N. I. 93 (1933) 159, *excl. syn.* — *B. linnaeana* C.CHR. Ind. Fil. Suppl. 3 (1934) 198; BACKER & POSTH. Varenfl. Java (1939) 80.

Cyrtogonium acuminatum BRACKENR. in Wilkes, U.S. Expl. Exp. 16 (1854) 86.

Poecilopteris stenophylla KURZ *ex* T. & B. Nat. Tijd. N. I. 27 (1864) 15; COPEL. Philip. J. Sc. 37 (1928) 393. — *B. stenophylla* CHING in C.Chr. Ind. Fil. Suppl. 3 (1934) 50.

Chrysodium heteroclitum (PRESL) KUHN *var. subcrenatum* KUHN, Ann. Mus. Bot. Lugd.-Bat. 4 (1869) 294, *p.p.*

Acrostichum modestum BAKER, J. Linn. Soc. 22 (1886) 231; C.CHR. in Copel. Philip. J. Sc. 37 (1928) 411. — *Leptochilus modestus* C.CHR. Ind. Fil. (1906) 386. — *Campium modestum* COPEL. Brittonia 1 (1931) 76, f. 1. — *B. modesta* CHING in C.Chr. Ind. Fil. Suppl. 3 (1934) 49.

Gymnopteris inconstans COPEL. in Perk. Fragm. Fl. Philip. (1905) 177; Polyp. Philip. (1905) 43. —

Leptochilus inconstans CHRIST, Bull. Herb. Boiss. II, 6 (1906) 1005. — *Leptochilus heteroclitus* (PRESL) C.CHR. *var. inconstans* CHRIST, Philip. J. Sc. 2 (1907) Bot. 160. — *B. inconstans* CHING in C.Chr. Ind. Fil. Suppl. 3 (1934) 48.

Leptochilus heteroclitus (PRESL) C.CHR. *var. eurybasis* CHRIST, Philip. J. Sc. 2 (1907) Bot. 159. — *Campium heteroclitum* (PRESL) COPEL. *var. eurybasis* COPEL. Philip. J. Sc. 37 (1928) 361.

Leptochilus heteroclitus (PRESL) C.CHR. *var. foxworthyi* CHRIST, Philip. J. Sc. 2 (1907) Bot. 160.

Leptochilus sumatranus v.A.v.R. Bull. Jard. Bot. Btzg II, 23 (1916) 15, pl. 2: f. 1a–c; Handb. Mal. Ferns, Suppl. 1 (1917) 436; *ibid.* Corrections (1917) 60.

Campium nigrum COPEL. Philip. J. Sc. 37 (1928) 361, f. 14, pl. 10. — *B. nigra* CHING in C.Chr. Ind. Fil. Suppl. 3 (1934) 49.

Campium pseudoscalpturatum COPEL. Philip. J. Sc. 37 (1928) 363, f. 16, pl. 11. — *B. pseudoscalpturata* CHING in C.Chr. Ind. Fil. Suppl. 3 (1934) 49; COPEL. Fern Fl. Philip. (1960) 261.

Campium foxworthyi COPEL, Philip. J. Sc. 37 (1928) 364, f. 17, pl. 12. — *B. foxworthyi* CHING in C.Chr. Ind. Fil. Suppl. 3 (1934) 48; COPEL. Fern Fl. Philip. (1960) 258.

Campium tenuissimum COPEL. Philip. J. Sc. 37 (1928) 364, f. 18, pl. 13. — *B. tenuissima* COPEL. Fern Fl. Philip. (1960) 259.

Leptochilus simplicifolius HOLTTUM, Gard. Bull. S. S. 4 (1929) 409. — *B. simplicifolia* CHING in C.Chr. Ind. Fil. Suppl. 3 (1934) 50; HOLTTUM, Ferns Malaya (1954) 464, f. 272.

Campium membranaceum COPEL. Philip. J. Sc. 40 (1929) 307, pl. 7. — *B. membranacea* C.CHR. Ind. Fil. Suppl. 3 (1934) 198; COPEL. Fern Fl. Philip. (1960) 261.

B. edanyoi COPEL. Philip. J. Sc. 81 (1952) 22, pl. 15; Fern Fl. Philip. (1960) 258.

Edanyoa difformis COPEL. Philip. J. Sc. 81 (1952) 22, pl. 17; Fern Fl. Philip. (1960) 265. — **Fig. 25d, 31a–g.**

Sterile fronds simple or pinnate, 15–100 cm long. *Pinnate fronds* 25–100 cm long; lamina index of non-flagelloid leaves 1–5, that of flagelloid leaves sometimes more, 10–> 75 by 5–30 cm, terminal segment to > 75 cm long, herbaceous, usually greenish, sometimes purplish; pinnae 2–10(–15), index 2–5(–7), 1–26 by 0.7–6.5 cm, base attenuate to truncate, margin usually ± entire, sometimes sinuate or sinuate-serrate or finely repand without teeth of spines; *terminal segment* usually ± conform to the pinnae, sometimes flagelloid; *venation pattern:* veins anastomosing into a ± regular pattern of variously large areoles, see fig. 31g. *Simple fronds* 15–45 cm long; lamina index 3–7(–17), 10–30 by (1–)2–7 cm, otherwise similar to the terminal segment of pinnate fronds. — *Fertile fronds* 14–75 cm long. *Pinnate fronds* 30–75 cm long; lamina index 1–4, pinnae index 2–7, 1–13 by 0.5–2.5(–4) cm. *Simple fronds* 14–40 (–> 45) cm long; lamina index 3–10, 4–13 by 0.5–2 cm. *Sporangia* inserted all over the lower surface. Spores with a smooth, cristate or cristate-undulate perispore. — Chromosomes n = 41, 2n = 82, *c.* 123.

Distr. E. India to S. Japan, Formosa, and Indo-China; in *Malesia:* throughout, except for the Lesser Sunda Is.; also in Micronesia (Caroline Is.) and Melanesia (Solomon Is.).

Ecol. On rocks, in soil or on bases of trees in moist places in rain-forest (often near streams), sometimes rheophytic, 0–1500(–1750) m.

Note. The morphological variation is outstanding. Throughout its area forms with simple fronds occur, *e.g. B. simplicifolia* from higher elevations in Malaya. In the Philippines several distinct vegetatively propagating dwarfs occur, *e.g. Edanyoa difformis* and *B. cuspidata.* Autoploidisation and hybridisation are common. Field studies are necessary to further unravel this aggregate.

8. Bolbitis sinuata (PRESL) HENNIPMAN, Blumea 18 (1970) 148; Leid. Bot. Ser. 2 (1977) 232, f. 61, 62. — *Polypodium ? sinuatum* PRESL, Rel. Haenk. 1 (1825) 21.

Acrostichum diversifolium BL. En. Pl. Jav. (1828) 103; Fl. Jav. Fil. (1829) 36, pl. 12. — *B. diversifolia* SCHOTT, Gen. Fil. (1835) *ad t.* 13; BACKER & POSTH. Varenfl. Java (1939) 84; HOLTTUM, Ferns Malaya (1954) 465; COPEL. Fern Fl. Philip. (1960) 258. — *Leptochilus diversifolius* C.CHR. Ind. Fil. (1906) 385; CHRIST, Philip. J. Sc. 2 (1907) Bot. 160, *quoad nomen solum*; v.A.v.R. Handb. Mal. Ferns (1908) 740. — *Campium diversifolium* COPEL. Philip. J. Sc. 37 (1928) 362, f. 15; BACKER & POSTH. Nat. Tijd. N. I. 93 (1933) 164.

Gymnopteris subsimplex FÉE, Hist. Acrost. (1845) 83, pl. 40: f. 3. — *Campium subsimplex* COPEL. Philip. J. Sc. 37 (1928) 356, f. 11, pl. 8; BACKER & POSTH. Nat. Tijd. N. I. 93 (1933) 159. — *B. subsimplex* CHING in C.Chr. Ind. Fil. Suppl. 3 (1934) 50; BACKER & POSTH. Varenfl. Java (1939) 81; COPEL. Fern Fl. Philip. (1960) 265.

[*Gymnopteris subrepanda* J. SMITH, Hook. J. Bot. 3 (1841) 403, *nomen.*] — *Poecilopteris subrepanda* PRESL, Epim. Bot. (1851) 171.

Anapausia zollingeri PRESL, Epim. Bot. (1851) 187. — *Leptochilus zollingeri* FÉE, Gen. Polyp. (1852) 55; v.A.v.R. Handb. Mal. Ferns (1908) 742, *p.p.*; *ibid.* Suppl. (1917) 436. — *Acrostichum zollingeri* KUNZE, Bot. Zeit. (1864) 419; COPEL. Philip. J. Sc. 37 (1928) 357. — *Chrysodium zollingeri* KUHN, Ann. Mus. Bot. Lugd.-Bat. 4 (1869) 293.

Acrostichum variabile HOOK. *var. rasamalae* RACIB. Pterid. Fl. Btzg (1898) 50.

Leptochilus hydrophyllus COPEL. Philip. J. Sc. 1 (1906) Suppl. 146. — *Campium hydrophyllum* COPEL. Philip. J. Sc. 37 (1928) 358, f. 12, pl. 9. — *B. hydrophylla* CHING in C.Chr. Ind. Fil. Suppl. 3 (1934) 48.

Leptochilus malaccensis C.CHR. Gard. Bull. S. S. 4 (1929) 394. — *B. malaccensis* CHING in C.Chr. Ind. Fil. Suppl. 3 (1934) 49; HOLTTUM, Ferns Malaya (1954) 470.

B. nitens HOLTTUM, Kew Bull. 13 (1958) 453; Ferns Malaya ed. 2 (1966) 635. — **Fig. 27j.**

Sterile fronds simple or pinnate, (8–)20–100 cm long. *Pinnate fronds* 35–100 cm long; lamina index 1–3, 25–60 by 8–40 cm, terminal segment 15–50 cm long, usually (sub)coriaceous, sometimes subcarnose, olivaceous or brownish; pinnae 2–11, index 3–10(–20), 5–35 by (0.5–)1–7 cm, base attenuate to truncate, margin entire or irregularly sinuate especially in the lower half, without teeth or spines throughout; *terminal segment* ± conform

to the central pinnae; *venation pattern:* veins anastomosing into a regular network of variously sized areoles, see fig. 27j. *Simple fronds* (8–)20–75 cm long; lamina index 3–10, (7–)20–60 by (1–)3–15 cm, otherwise like the terminal segment of pinnate fronds. — *Fertile fronds* (8–)20–90 cm long. *Pinnate fronds* 30–90 cm long; lamina index 1–4, pinnae index 4–10(–16), 5–17 by (0.5–)0.7–3 cm. *Simple fronds* (8–)20–60 cm long; lamina index 5–18, (4–)8–35 by (0.3–)0.5–4 cm. *Sporangia* inserted all over the lower surface. Spores with a smooth cristate perispore. — Chromosomes n = 41, 2n = 122 + fragm.

Distr. India (Nicobar Is.) and Peninsular Thailand; in *Malesia:* Sumatra, Malay Peninsula, W. Java, Borneo, Philippines, New Guinea (in W. and NE. each one collection). Fig. 32.

Ecol. Terrestrial and low-epiphytic in evergreen forest, 0–1200(–1800) m.

Note. In the Malay Peninsula HOLTTUM recognized two quite distinct forms, *B. malaccensis* and *B. nitens*.

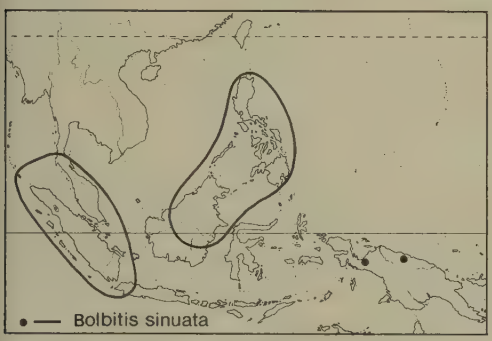

Fig. 32. Range of *Bolbitis sinuata* (PRESL) HENNIPMAN.

4. Series Quoyanae

HENNIPMAN, Leid. Bot. Ser. 2 (1977) 250.

Sterile fronds usually pinnate, rarely simple; petiole with 3–16 vascular bundles; lamina with one subterminal bulbil; pinnae up to 52, the margin with or without spines; terminal segment triangular; venation pattern: veins regularly reticulate, areoles angulate, ± isodiametric or elongate, decreasing in size towards the margin. Spores with a smooth, cristate or cristate-undulate perispore. — Chromosomes n = 41, 2n = 82, 123.

Distr. *E. Malesia*, Pacific, Japan (Bonin Is.).

9. Bolbitis quoyana (GAUDICH.) CHING in C.Chr. Ind. Fil. Suppl. 3 (1934) 49; BACKER & POSTH. Varenfl. Java (1939) 81, *p.p.*; COPEL. Fern Fl. Philip. (1960) 264; HENNIPMAN, Leid. Bot. Ser. 2 (1977) 250, f. 69, 70. — *Acrostichum quoyanum* GAUDICH. in Freyc. Voy. Uranie (1827) 306, pl. 3; HOOK. Sp. Fil. 5 (1864) 259. — *Gymnopteris repanda* (BL.) CHRIST *var. quoyana* (GAUDICH.) DIELS in K.Sch. & Laut. Fl. Schutzgeb. (1900) 117. — *Leptochilus cuspidatus* (PRESL) C.CHR. *var. quoyanus* C.CHR. *ex* V.A.V.R. Handb. Mal. Ferns (1908) 742, *p.p.*; BRAUSE, Bot. Jahrb. 56 (1920) 117. — *Campium quoyanum* COPEL. Philip. J. Sc. 37 (1928) 366, f. 20a, *p.p.*; BACKER & POSTH. Nat. Tijd. N. I. 93 (1933) 161, *p.p.*

Heteroneuron naumannii KUHN, Forsch. Reise Gazelle 4, Farne (1889) 5, pl. 1. — *Gymnopteris naumannii* DIELS in K.Sch. & Laut. Fl. Schutzgeb. (1900) 117. — *Leptochilus naumannii* C.CHR. Ind. Fil. (1906) 386; V.A.V.R. Handb. Mal. Ferns (1908) 742; BRAUSE, Bot. Jahrb. 56 (1920) 118. — *B. naumannii* CHING in C.Chr. Ind. Fil. Suppl. 3 (1934) 49.

Leptochilus cuspidatus (PRESL) C.CHR. *var. marginalis* ROSENST. in Fedde, Rep. 9 (1911) 426; V.A.V.R. Handb. Mal. Ferns Suppl. (1917) 435; BRAUSE, Bot. Jahrb. 56 (1920) 117.

Aspidium novo-pommeranicum BRAUSE *ex* RECH. Denkschr. K. Ak. Wiss. M.-N. Kl. Wien 89 (1914) 471, pl. 3: f. 8b.

Campium validum COPEL. Philip. J. Sc. 37 (1928) 369, f. 22, pl. 15.

Campium parvum COPEL. Philip. J. Sc. 37 (1928) 375, f. 28, pl. 21. — *B. parva* CHING in C.Chr. Ind. Fil. Suppl. 3 (1934) 49.

Campium enorme COPEL. Philip. J. Sc. 40 (1929) 307, pl. 8. — *B. enormis* C.CHR. Ind. Fil. Suppl. 3 (1934) 197; COPEL. Fern Fl. Philip. (1960) 264.

Campium viviparum KJELLB. in C.Chr. Bot. Jahrb. 66 (1933) 50. — *B. vivipara* C.CHR. Ind. Fil. Suppl. 3 (1934) 51.

Stenosemia dimorpha COPEL. Philip. J. Sc. 84 (1955) 161, pl. 1.

[*Cyrtogonium laciniatum* J. SMITH, Hook. J. Bot. 3 (1841) 403, *nomen.*] — **Fig. 31h–k.**

Sterile fronds pinnate, up to 130 cm long; lamina index 1–3(–4), up to 80 by 40 cm, terminal segment 9–26 cm long, herbaceous to subcoriaceous, green or brown (or blackish); pinnae 13–52, index 2–7, 7–22 by 1.3–3.5(–4.5) cm, base symmetrical, (narrowly to) broadly cuneate to cordate, margin usually lobed $^1/_3$–$^2/_3$ towards the costa, sometimes either ± entire or lobed to $^4/_5$ towards the costa, with a usually rather inconspicuous spine in the sinuses, apex acute to acuminate, lobes close together to spaced, straight or subfalcate, margin entire or crenate-serrate; *terminal segment* narrowly triangular, shorter than the remaining part of the lamina; *venation pattern:* veins forming a regular network, areoles angulate isodiametric or elongate decreasing in size towards the margin, see fig. 31j–k. *Fertile fronds* up to 120 cm long; lamina index 3–6, pinnae index 5–15, 3–15 by 0.4–1.7 cm. *Sporangia* usually inserted all over the lower surface, sometimes situated along the margin only, the arrangement usually acrostichoid, sometimes ± pteridoid. Spores with a smooth cristate perispore. — Chromosomes n = 41, 2n = 82, 123.

Distr. Queensland, Polynesia (Samoa, Fiji), Melanesia (Solomons), Micronesia (Bonin Is.); in *Malesia:* New Guinea (common, also in the Bismarcks), Moluccas (P. Pisang, Halmaheira, Ternate, Morotai), Philippines, Celebes, Central & West Java. Fig. 33.

Ecol. On rocks and in soil in rain-forest, mostly near streams; several times reported from limestone; 0–1200(–1700) m.

Note. The species has been confused with *B. repanda*. It is closest to *B. rivularis*, its coriaceous counterpart (and also showing a tendency to dwarfing), and to *B. taylorii*, an endemic from Queensland.

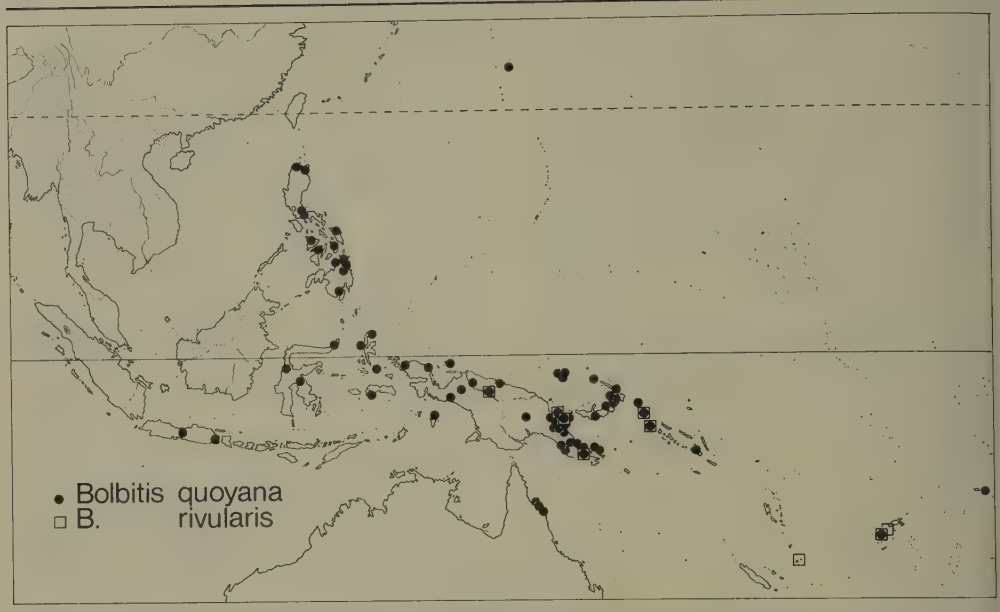

Fig. 33. Range of *Bolbitis quoyana* (GAUDICH.) CHING and *B. rivularis* (BRACKENR.) CHING.

10. Bolbitis rivularis (BRACKENR.) CHING in C.Chr. Ind. Fil. Suppl. 3 (1934) 50; BACKER & POSTH. Varenfl. Java (1939) 82 ('*B. ? rivulare*'); HENNIPMAN, Leid. Bot. Ser. 2 (1977) 255, f. 70, 71. — *Cyrtogonium rivulare* BRACKENR. in Wilkes, U.S. Expl. Exp. 16 (1854) 85, pl. 11: f. 2. — *Leptochilus rivularis* C.CHR. Ind. Fil. (1906) 387. — *Campium rivulare* COPEL. Philip. J. Sc. 37 (1928) 373, f. 27, pl. 20; BACKER & POSTH. Nat. Tijd. N. I. 93 (1933) 161.

Campium kajewskii COPEL. Philip. J. Sc. 60 (1936) 112, pl. 22.

Sterile fronds usually pinnate, rarely simple, 10–70 cm long. *Pinnate fronds* 10–70 cm long; lamina index 1–3(–5), 7–40 by 3–25 cm, terminal segment 5–30 cm long, fleshy-coriaceous, olivaceous to brownish; pinnae 2–11, index 1–5, 1.5–16 by 0.8–4.5 cm, base ± symmetrical, cuneate to subcordate, margin ± entire to lobed to $^1/_5(-^2/_5)$ towards the costa, without or with but an inconspicuous tooth or spine in the sinuses; *terminal segment* triangular, as long as to longer than the remaining part of the lamina; *venation pattern:* veins forming a regular network of angulate, isodiametric or elongate areoles which decrease in size towards the margin. *Simple fronds* 15–30 cm long, lamina index 4–7, 12–23 by 2.5–4.5 cm, base cuneate to subcordate, margin ± entire to lobed to $^2/_5$ towards the costa, otherwise similar to the terminal segment of pinnate fronds. — *Fertile fronds* pinnate, 20–75 cm long; lamina index 1–4, pinnae index 1–6, 1.2–9 by 0.3–1.5 cm. *Sporangia* inserted all over the lower surface. Spores with a smooth cristate perispore. — Chromosomes n = 41.

Distr. Polynesia (Fiji), Melanesia (Solomons, New Hebrides); in *Malesia:* New Guinea (West: 2 collections; East). Fig. 33.

Ecol. Terrestrial and on rocks in moist places in rain-forest; several times reported to grow near or in streams, 0–2000 m.

Note. The species is not rarely found fertile with small leaves composed of a large terminal segment and two small pinnae. Dwarfs grow massed on rocks in rivers in New Guinea.

Species incertae sedis

11. Bolbitis novoguineensis HENNIPMAN, Leid. Bot. Ser. 2 (1977) 270, f. 74k–n. — **Fig. 31l.**

Sterile fronds pinnate, 9–21 cm long; lamina index 3–5, 7–17 by 2–4 cm, terminal segment 1.5–4 cm long, firm-herbaceous (to subcarnose?), olivaceous, with a ± terminal bulbil; rachis with a narrow wing throughout or in the upper half only; pinnae > 16 to 30, index 1–3, 1–2.4 by 0.7–0.8 cm, base usually symmetrical, cuneate, sometimes somewhat asymmetrical, its basiscopic side cuneate, the acroscopic side either broadly attenuate or with a basal acroscopic lobe, margin (bi)crenate-serrate with distinct spines in the sinuses; *terminal segment* usually narrowly triangular, much shorter than the remaining part of the lamina, the basal half with few lobes, tapering towards the acute or short-flagelloid apex, sometimes the whole terminal segment flagelloid; *venation pattern:* veins usually forming a costal areole, sometimes locally free. *Fertile fronds* 15–> 20 cm long; lamina index *c.* 10, pinnae index 4–6, 0.6–0.8 by *c.* 0.2 cm. *Sporangia* inserted all over the lower surface. Spores with a smooth cristate perispore.

Distr. *Malesia:* E. New Guinea (D'Entrecasteaux Is.), 3 collections.

Ecol. Creeping on rocky banks of streams in rain-forest, 250 and 900 m.

Note. A small thickening presumably representing a primordium of a bulbil is found terminally on the costae.

12. Bolbitis repanda (BL.) SCHOTT, Gen. Fil. (1835) *ad t.* 13; HENNIPMAN, Leid. Bot. Ser. 2 (1977) 274, f. 78. — *Acrostichum repandum* BL. En. Pl. Jav. (1828) 104; Fl. Jav. Fil. (1829) 39, pl. 14, 15, *p.p.* — *Campium repandum* PRESL, Tent. Pterid. (1836) 239. — *Gymnopteris repanda* CHRIST, Farnkr. Erde (1897) 50, *p.p.*; DIELS in E. & P. Nat. Pfl. Fam. 1, 4 (1901) 201, *p.p.*; COPEL. Publ. Bur. Gov. Lab. 28 (1905) 43, *p.p.* — **Fig. 27i.**

Sterile fronds pinnate, 35–100(–120) cm long; lamina index of non-flagelloid fronds 1–3, of flagelloid fronds up to 7, 15–70(–100) by 6–30 cm, terminal segment 8–60(–70) cm long, herbaceous-pergamentaceous, green to blackish, with a (primordium of a) spherical subterminal bulbil; pinnae 8–20(–24), index (2–)3–6(–8), 4.5–22 by 1.5–4.5 cm, base ± symmetrical, angustate to broadly cuneate, margin lobed $^1/_4$–$^1/_2$ towards the costa, usually with a distinct tooth in each sinus, lobes usually finely serrate-crenate, sometimes entire; the two lowermost pinnae ± conform to the pinnae; *terminal segment* triangular; *venation pattern* irregular, veins forming areoles varying in shape and size, some of which with usually one, mostly excurrent included free vein, see fig. 27i. *Fertile fronds* 35–85 cm long; lamina index 2–5, pinnae index 3–9, 1.5–7 by 0.4–1.5(–2) cm. *Sporangia* inserted all over the lower surface. Spores with a smooth cristate-undulate perispore. — Chromosomes n = 82, 2n = *c.* 120.

Distr. Micronesia (one record from the Marianas); in *Malesia:* Philippines (Luzon, Mindanao), Borneo (Sabah, Sarawak), Celebes, Lesser Sunda Is. (Bali to Flores).

Ecol. Usually terrestrial, sometimes low-epiphytic, in forest, 125–1650 m.

Note. Presumably of hybrid origin. The irregular venation pattern shows considerable variation and includes all intermediates between a venation pattern as found in *B. sinensis* or *B. rhizophylla* (both *ser. Egenolfianae*) and one as found in *B. heteroclita* (*ser. Heteroclitae*).

Hybrids

H. 1. Bolbitis × arguta (FÉE) CHING in C.Chr. Ind. Fil. Suppl. 3 (1934) 47; COPEL. Fern Fl. Philip. (1960) 263, *p.p.*, *p. spec.*; HENNIPMAN, Leid. Bot. Ser. 2 (1977) 288, f. 83i, j. — *Heteroneuron argutum* FÉE, Hist. Acrost. (1845) 96, pl. 25: f. 2, *p.p.*; PRESL, Epim. Bot. (1851) 169. — *Campium argutum* COPEL. Philip. J. Sc. 37 (1928) 376, *p.p.*

Fronds small, pinnate throughout or the basal part bipinnate, with a triangular terminal segment. *Sterile fronds:* lamina with a subterminal bulbil; pinnae irregularly and variously lobed, pinnae of one pair sometimes much different, odd pinnae present in part of the material. *Fertile fronds:* sporangia inserted all over the lower surface. Spores abnormal or sporangia with aborted spore-mother-cells.

Distr. *Malesia:* Philippines (Luzon), known from the type collection only.

Parentage. I have doubts whether this fern warrants a separate treatment as a hybrid; it may be close to *Edanyoa difformis* (= *B. heteroclita*).

H. 2. Bolbitis heteroclita × rhizophylla HENNIPMAN, Leid. Bot. Ser. 2 (1977) 291, f. 83l–o.

Sterile fronds pinnate, with a subterminal bulbil; rachis with or without narrow wing; pinnae 16–24, index 3–5, 4.5–6 by 1.2–1.6 cm, base truncate to cuneate, margin usually ± entire, sometimes irregularly and finely serrate or with a few incisions about halfway towards the costa, with distinct spines; *terminal segment* triangular, deeply lobed near the base; *venation pattern* irregular, veins forming a costal areole (rarely lacking), sometimes also one or a few smaller distal areoles. *Fertile fronds:* pinnae index 2–5, 1.6–4 by 0.6–0.8 cm. *Sporangia* inserted mainly on the veins. Spores abnormal, or with aborted spore-mother-cells. — Chromosomes 2n = 82; at meiosis univalents only.

Distr. *Malesia:* Philippines (Luzon, Mt Maquiling, 2 collections).

Ecol. A shady place in forest, at 350–400 m.

H. 3. Bolbitis × singaporensis HOLTTUM, Gard. Bull. S. S. 11 (1947) 271; Ferns Malaya (1954) 467, f. 274; HENNIPMAN, Leid. Bot. Ser. 2 (1977) 296, f. 85a–d.

B. quoyana auct. non (GAUDICH.) C.CHR.: HOLTTUM, Gard. Bull. S. S. 9 (1937) 122. — **Fig. 27n.**

Sterile fronds pinnate, 35–70 cm long; lamina index 1–3, 22–45 by 10–25 cm, terminal segment 10–19 cm long, firm-herbaceous, bright green to olivaceous, with a subterminal bulbil; rachis not winged; pinnae 14–27, index 3–5, 5.5–12.5 by 1.5–3 cm, base varying from ± symmetrical, subcordate, cuneate or angustate, to (strongly) oblique with its acroscopic side much better developed and provided with a distinct basal acroscopic lobe (or auricle), margin entire to lobed to $^1/_7$(–$^1/_4$) towards the costa, with a more or less distinct spine in (some of) the sinuses; *terminal segment* triangular; *venation pattern* very irregular: veins forming a costal areole (rarely lacking), with or without few to several smaller distal areoles varying in size and shape, the areoles with or without usually one excurrent included free vein, see fig. 27n. *Fertile fronds* 50–70 cm long; pinnae index 4–8, 2–6.5 by 0.4–1.2 cm. *Sporangia* inserted mainly on the veins. Spores abnormal, or sporangia with aborted spore-mother-cells. — Chromosomes 2n = 82; at meiosis univalents only.

Distr. *Malesia:* Malay Peninsula (Singapore, Fern Valley on Bt Timah).

Ecol. On granite rocks in stream-bed, in the shade of primitive forest.

Parentage. MANTON (in Holttum, 1954) correctly suggested this to be a hybrid between *Egenolfia appendiculata* (= *B. appendiculata ssp. appendiculata*) and *B. diversifolia* (= *B. sinuata*). These two species and the hybrid grow intermingled in the Fern Valley on Bt Timah.

H. 4. Bolbitis × sinuosa (FÉE) COPEL. Fern Fl. Philip. (1960) 262; HENNIPMAN, Leid. Bot. Ser. 2 (1977) 298, f. 85e–p. — *Heteroneuron sinuosum* FÉE, Hist. Acrost. (1845) 95; COPEL. Philip. J. Sc. 37 (1928) 368, f. 21.

B. × *foxii* COPEL. Philip. J. Sc. 81 (1952) 22; Fern Fl. Philip. (1960) 263. — **Fig. 27m.**

Distr. *Malesia:* Philippines (Luzon, Mindanao, Central Polillo).

Parentage. *B. quoyana* and possibly *B. rhizophylla* or *B. heteroclita*.

Two nothomorphs are distinguished.

a. *nm.* **sinuosa** HENNIPMAN, Leid. Bot. Ser. 2 (1977) 299, f. 85e, f.

Sterile fronds pinnate, up to 50 cm long; lamina index 1–2, 16–32 by 10–18 cm, terminal segment 8–12 cm long, herbaceous, dark olivaceous or brown, with or without a spherical subterminal bulbil; pinnae 13–20, index 5–7, 7.5–12 by 1.1–1.8 cm, base symmetrical, narrowly cuneate, margin shallowly and oblique lobed or finely crenate-serrate, with small teeth in the sinuses; *terminal segment* triangular; *venation pattern:* veins forming a costal areole and several smaller distal ones, the areoles without included free veins. *Fertile fronds:* pinnae *c.* 5 by 0.7–0.9 cm. *Sporangia* inserted all over the lower surface. Spores abnormal or sporangia with aborted spore-mother-cells.

Distr. *Malesia:* Philippines (Luzon, 3 localities).

b. *nm.* **foxii** (COPEL.) HENNIPMAN, Leid. Bot. Ser. 2 (1977) 299, f. 85g–p. — *B.* × *foxii* COPEL. Philip. J. Sc. 81 (1952) 22.

If compared with *nm. sinuosa* the plants are of the same size or smaller, with smaller and generally also narrower pinnae with a somewhat simpler venation pattern, see fig. 27m. — Chromosomes 2n = *c.* 80.

Distr. *Malesia:* Philippines (3 collections from Polillo I., Luzon, and Mindanao).

Hybridae incertae sedis

H. 5. Leptochilus × **trifidus** v.A.v.R. Bull. Dép. Agr. Ind. Néerl. 18 (1908) 26; HENNIPMAN, Leid. Bot. Ser. 2 (1977) 300, f. 85q–w.

Hemigramma latifolia auct. non COPEL.: COPEL. Philip. J. Sc. 37 (1928) 404, *p.p.* — **Fig. 27l.**

Sterile fronds simple, either entire or trifid, 30–60 cm long, firm-herbaceous to subcoriaceous, brownish, with a small but conspicuous subterminal bulbil, base narrowly cuneate or angustate, gradually or abruptly decurrent on the petiole, margin entire or slightly sinuate; *venation pattern* rather irregular, see fig. 27l. *Fertile fronds* 25–50 cm long. *Sporangia* inserted all over the lower surface. Spores usually shrivelled, normally shaped spores with a smooth, (imperfectly developed) cristate-undulate or cristate perispore.

Distr. *Malesia:* Sumatra (3 localities in West Coast, East Coast, and Bencoolen).

Ecol. Forest; reported from rocks either in streams or on stream-banks, (one record) 450–500 m.

Parentage. *B. sinuata* and possibly *Leptochilus decurrens*. A very interesting hybrid which needs experimental study.

Species dubiae

D. 1. Bolbitis interlineata (COPEL.) CHING in C.Chr. Ind. Fil. Suppl. 3 (1934) 48; ITO, J. Jap. Bot. 14 (1938) 439, *quoad nomen solum*; HENNIPMAN, Leid. Bot. Ser. 2 (1977) 306, f. 86g, h. — *Campium interlineatum* COPEL. Philip. J. Sc. 37 (1928) 370, f. 24, pl. 17. — **Fig. 27k.**

Sterile fronds pinnate, 60–75 cm long; lamina index 1–2, 30–40 by 20–24 cm, terminal segment 12–20 cm long, herbaceous, with a spherical subterminal bulbil; pinnae 8–16, index 3–5, 13.5–15 by 3–4 cm, base either ± symmetrical, broadly cuneate to subcordate, or asymmetrical with its basiscopic side longer and/or wider than its acroscopic side, margin entire or (in part) slightly sinuate; *terminal segment* ± conform to the pinnae or triangular with 1–2 basal lobes; *venation pattern* very intricate, reminiscent of that of *B. heteroclita* but part of the areoles with usually one excurrent included free vein, see fig. 27k. *Fertile fronds* 60–85 cm long; lamina index 2–4, pinnae index 5–8, 5–6 by 0.7–1 cm. *Sporangia* all over the lower surface. Spores with a smooth cristate perispore.

Distr. *Malesia:* Borneo (Sarawak: Bungo Range, Mt Matang, and Mt Penrissen).

Ecol. Forest; on rocks in streams, 300–690 m.

Note. Possibly of hybrid origin and related to *B. heteroclita* (venation pattern!) and to either *B. scalpturata* or *B. repanda*.

D. 2. Leptochilus stolonifer CHRIST, Bull. Herb. Boiss. II, 6 (1906) 1004; v.A.v.R. Handb. Mal. Ferns (1908) 739.

Distr. *Malesia:* Philippines (Angilog), type only.

Note. Possibly synonymous with *B. heteroclita* but the venation pattern as given by CHRIST is deviating. Type not traced.

Excluded

Bolbitis ovata (COPEL.) CHING in C.Chr. Ind. Fil. Suppl. 3 (1934) 49. — *Leptochilus ovatus* COPEL. Philip. J. Sc. 9 (1914) Bot. 229. — *Campium ovatum* COPEL. Philip. J. Sc. 28 (1937) 354, f. 9, pl. 6. — *Paraleptochilus ovatus* COPEL. Gen. Fil. (1947) 198. — Type: C. J. BROOKS 155 S, Sumatra, Bencoolen, Lebong Tandai, ii–1913 (iso in BM) = *Colysis cf. pedunculata* (HOOK. & GREV.) CHING.

Bolbitis subcrenata (HOOK. & GREV.) CHING; HENNIPMAN, Leid. Bot. Ser. 2 (1977) 176, f. 46, 47.

BACKER & POSTHUMUS (Varenfl. Java, 1939, 80; Nat. Tijd. N. I. 93, 1933, 158, *pro Campium subcrenatum*) reported this fern from Java. The material traced belongs to *B. subcrenata var. prolifera* (endemic in Ceylon) and is presumably cultivated.

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